

**Energy Research and Development Division
FINAL PROJECT REPORT**

**ASSESSING LONG-TERM DYNAMICS
OF BIRD DISTRIBUTIONS IN
RELATION TO CLIMATE CHANGE:
FROM GRINNELL TO PRESENT**

Prepared for: California Energy Commission
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PREFACE

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ABSTRACT

Certain renewable energy technologies, such as solar and wind, can use large areas of land and may have ecological impacts that must be mitigated, for example, setting aside other areas of similar ecological importance. Current analyses assume that historical distribution of species can inform the selection of the mitigation areas. However, climate change invalidates this assumption. For this reason, ecological impacts and mitigation efforts should consider how climate change will affect the distribution of flora and fauna. Scientists expect ranges of many species to shift dramatically with future climate change. Long-term range shifts and species colonization and extinction (turnover) events are best understood by comparing historical surveys to modern surveys. The authors used mean annual temperature and annual precipitation data to test for effects of climate change and land use change over the last 100 years on the distribution patterns of 100 breeding bird species, primarily songbirds. Joseph Grinnell and colleagues first surveyed sites along a 1,000 km north-south transect in the California Coast Ranges between 1911 and 1940. The authors resurveyed 70 of these sites for this project in 2009 and 2010. Occupancy models were used to estimate detectability and site-level measures of occupancy, colonization, and extinction between the two survey periods.

With a better understanding of sensitivity of birds to climate change and land-use, wildlife managers and energy industry planners will effectively know which indicators to consider when planning for the preservation of birds and locating power generation facilities. Advanced planning for conservation areas will help energy providers site new facilities more quickly and economically, as well as decrease negative impacts on California's wildlife.

Keywords: California Coast Range, climate change, colonization, detection probability, Grinnell Resurvey Project, historical data, land use, local extinction, occupancy modeling, passerines, resurvey, site occupancy, species turnover

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EXECUTIVE SUMMARY

Introduction

Certain renewable energy technologies, such as solar and wind, may require significant amounts of land. For those facilities sited in areas with sensitive species and habitats, mitigation of these ecological impacts is often required. One common mitigation approach is through set aside of other areas of similar ecological importance. Current analyses assume that historical distribution of species can inform the selection of the mitigation areas. However, climate change invalidates this assumption. For this reason, ecological impacts and mitigation efforts should consider how climate change will affect the distribution of flora and fauna.

Human-driven climate change has contributed to the ranges of birds growing, shrinking, or shifting. The impacts of climate change on plants and animals are projected to continue and are likely to be further accelerated by habitat fragmentation and loss. The authors examine changes in bird distribution patterns in the California Coast Ranges by comparing bird survey data gathered between 1911 and 1940 to modern resurveys conducted in 2009 and 2010. The authors tested whether a century of change in climate or land use had the most effect on bird distributions.

The study produced a dataset of bird occupancy through strategic resurveys of birds at sites with different climate change histories originally sampled 70 to 99 years ago; (2) produce estimates of occupancy for 100 bird species that accounted for differences in the likelihood each species would be detected at different sites, between the historical and modern eras, and by different observers; and (3) rank the ability of various climate change and land use factors to “explain” changes (in the statistical sense) bird distribution patterns in the study area over the past century.

The authors predicted bird species turnover (colonization or extinction) to be highest at sites where the climate changed the most, where land use changed the most, or both. In response to climate warming, ranges of birds were expected to shift northward, upslope, or toward the coast where the ocean may help to lessen changes in climate.

Methods

The historical dataset was assembled and consists of local habitat descriptions and quantitative, repeated daily bird surveys conducted during the breeding season. The authors picked sites for resurvey that were historically surveyed multiple times. They revisited 70 sites in 20 counties of the California Coast Ranges. The 70 sites had 347 historical surveys and 216 modern surveys.

The resurvey consisted of systematic bird inventories, noting each bird seen or heard within a seven-minute period during the 2009 and 2010 breeding seasons. Each site consisted of approximately 10 stations along a two to three km transect.. Sites were visited three or more times within a single season.

The authors modeled the effects of climate change and land use change on the local colonization and extinction processes of the birds in the California Coast Ranges. Seven variables and

variable combinations were tested to determine which factors were most associated with colonization and extinction probabilities. Predictor variables consisted of the changes in mean annual temperature and in mean precipitation between eras, a human influence index that described modern land use intensity, and their combined effects. Of the 70 sites, 65 experienced warming from the historical to modern era; the other 5 experienced cooling. Only 6 of the 70 sites experienced less precipitation in the modern era than in the historical era.

The research team also examined patterns of colonization and extinction for groups of species (songbirds, raptors, woodpeckers, others), resident vs. nonresident songbird, foraging type (insectivore, granivore, omnivore, other), nest type (cup, cavity, other), clutch size, and body mass. The research team tested whether the primary predictor(s) of colonization and extinction across species groups were statistically different. Project Results

Results

More bird species were detected in the modern era (199) than in the historical era (174). Of the 220 total species detected in the historical and modern surveys, 153 were detected in both eras. Apparent colonization and extinction of species at sites appeared to be frequent. Probabilities of detection for species were significantly greater for modern than historic surveys and were most influenced by differences among observers. Because the historical probability of detection was lower than the modern counterpart, the authors are less confident in the probability of a site becoming colonized than going extinct.

Estimates of occupancy changed little over a century for about half (53) of the 100 bird species. For the other half, however, about twice as many species decreased (32) in occupancy by greater than 10 percent as those that increased in occupancy by greater than 10 percent (15). Anna's Hummingbird had the largest increase in the probability of occupancy (60 percent). Tree swallows had the largest decrease in probability of occupancy (40 percent).

Colonization and extinction varied by species and depended on numerous factors. Land-use intensity, change in temperature, and change in precipitation, either singly or combined, were associated with local colonization for 54 percent of the species and local extinction for 60 percent of the species. Turnover was not associated with these factors for about one-third of the species. Of those species whose colonization or extinction could be related to a factor, more were associated with climate change (i.e., change in temperature, change in precipitation, or change in both) than by land use alone. As expected, turnover factors increased the likelihood of colonization and extinction for some species and decreased it for others. Factors affecting colonization and extinction were not significantly associated with groups of species, foraging type, or life history traits.

Discussion

On average, species were more likely to go extinct at sites that became hotter and to colonize sites that became wetter. Land-use intensity did not have as strong an effect on the local colonization or extinction. Species turnover was greatest at sites that warmed, occurring at northerly latitudes and lower elevations. Turnover at northern latitudes may reflect changes in the species whose range limits are in the northern portion of the study area. Higher turnover at

lower elevation may be associated with more intense land use and higher human population density there, such as the San Francisco Bay Area. As land-use intensity and climate change continue to increase in the future, their effects on the species in this study may well become even greater. Basic biological differences in each of the 100 breeding bird species the authors analyzed within the California Coast Ranges led to different colonization and extinction responses to changing climate and land-use intensity.

Range shifts, whether related to climate change or other factors, are primarily expected to be detected over an elevational range or at the edges of a species range. Although the study area extended from sea level to an elevation of 1800m, this range was not large enough to expect much upslope movement in response to climate warming. It is likely that this sampling design would have masked any elevational shift that may have occurred. Furthermore, very few species that the authors analyzed have range limits within the California Coast Ranges study area. Given these challenges, it is remarkable that these analyses were able to associate many observed changes in bird distributions to the climate change factors.

Historical data of species distribution are incredibly valuable in understanding how and why distributions change and why they may be different in the future. However, historical data often have limitations, such as inconsistent historical survey methods. Occupancy models helped overcome some limitations and ultimately provided an understanding of the mechanisms that best explained colonization and extinction events. This analytical framework yielded improved estimates of occupancy in the historical and modern eras, given differences in the likelihood of detecting each species between sites, between the historical and modern eras, and between observers. Another difficulty in working with this historical dataset was that historical vegetation and land-use data were not available for the survey area. The authors addressed this issue by resurveying sites where these characteristics appeared to be similar now to descriptions in the field notes.

Conclusion

The authors found a large percentage of the 100 bird species analyzed had already experienced local colonization and extinction related to climate effects (25.5 percent), land-use effects (19 percent), or a combination of these factors (13 percent). Of the climate variables, turnover was more strongly associated with change in temperature than in precipitation, although both were relevant. Importantly, colonization was more likely at sites that got wetter and extinctions more likely at sites that got hotter. Species may be experiencing climate-related effects beyond those the research team detected, such as the timing of migration and breeding. The diverse topography in the California Coast Ranges may enable some species to better cope with climate change by tracking their climatic niche as it shifts across the landscape. While the authors sampled only sites that had experienced relatively low levels of land use change, the authors expect that land-use change would be a more important driver of colonization and extinction with more intense land use.

Benefits to California

Bird extinctions and range shifts are expected to become more frequent as climate change and habitat loss and fragmentation continue. Although none of the species examined here have gone completely extinct, birds in the study area generally had a lower probability of occupancy in the resurvey period than in the historical survey period. A continued decrease in local colonization rates and increase in local extinction rates may have similar consequences as those expected from species extinctions: a decrease in ecosystem services that benefit Californians, including decomposition, seed dispersal, pollination, and control of insect populations. With a better understanding of sensitivity of birds to climate change and land-use, wildlife managers and energy industry planners will effectively know which indicators to consider when planning for the preservation of bird species and habitats and siting power generation facilities. Advanced planning for conservation areas will help energy providers site new facilities more quickly and economically, as well as decrease negative impacts on California's wildlife.

CHAPTER 1:

Assessing Long-Term Dynamics of Bird Distributions in Relation to Climate Change: From Grinnell to Present

1.1. Introduction

Human-driven climate change (IPCC 2007) has clearly affected the phenology of species and contributed to range expansions and contractions (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006, Thomas et al. 2006, Tingley et al. 2009). Recent model-based predictions of how faunal ranges will respond to future climate change are truly alarming (Peterson et al. 2002, Williams et al. 2003, Thomas et al. 2004, Malcolm et al. 2006). They frequently predict large range shifts, high global extinction rates, and reorganized communities (Thomas et al. 2004, Williams and Jackson 2007, Stralberg et al. 2009), and raise questions about the capacity of even large protected areas to sustain diversity (Burns et al. 2003). The projected impacts of climate change on biodiversity are likely to be further exacerbated by habitat fragmentation and habitat loss (Fahrig 2003, Gaston et al. 2003, Şekercioğlu et al. 2004, Brook et al. 2008).

Despite their recent prominence and impact, models that predict outcomes of climate-change are highly uncertain (Davis et al. 1998, Araujo et al. 2005, Lawler et al. 2006, Pearson et al. 2006, Elith & Leathwick 2009). These bioclimatic- or habitat-based models are subject to many sources of error (Beissinger & Westphal 1998, Thuiller 2004, Harte et al. 2004, Guisan & Thuiller 2005). The most direct way to test the accuracy of model predictions of the effects of climate change on species' distributions is to apply models to predict response to observed climate change between that time and the present, and then test the models using appropriately stratified and independent survey data from the present. The challenge is to identify historical records with the necessary precision, geographic and temporal scale, and magnitude of observed climate change (Root & Schneider 1995, Pearson & Dawson 2003, Rowe 2005, Guisan & Thuiller 2005, Walther et al. 2005).

Most analyses of changes in species' distribution or phenology have been conducted from the 1960's onwards (e.g., Winkler et al. 2002, Root et al. 2005, Wilson et al. 2005, Hickling et al. 2006, Menzel et al. 2006), and thus are subject to meso-scale climatic fluctuations such as the Pacific Decadal or North Atlantic Oscillations (Walther et al. 2002, Millar et al. 2004) or time-lagged responses (Menendez et al. 2006). Such results can also be confounded by landscape modification (Hickling et al. 2006, Jetz et al. 2007). Furthermore, range shifts are uncertain when plagued by false absences due to limited historic sampling and inability to control for changes in detectability between historic and current sampling periods (Hill et al. 2002, Shoo et al. 2005). Historic data are generally required to document long-term range shifts and species turnover events (Moritz et al. 2008, Tingley and Beissinger 2009, Tingley et al. 2009).

California is fortunate to have a unique historical record that enables the examination of changes in patterns of diversity over the past 100 years. Between 1904 and 1940, Joseph Grinnell and colleagues documented and systematically collected terrestrial vertebrates from >700 locations on multiple transects spanning the environmental diversity of California. This effort resulted in a remarkable snapshot of early 20th century vertebrate diversity which includes >100,000 specimens, 74,000 pages of field notes including standardized bird count data and habitat (including vegetation) observations, and 10,000 images.

The authors examine changes in avian distribution patterns in the California Coast Range by comparing bird survey data gathered between 1911 and 1940 by Grinnell and colleagues to modern resurveys that the authors conducted in 2009 and 2010. The research team used occupancy modeling approaches to test whether changes in bird distributions were best explained by a century of climate change or by changes in land use. By mining the historic field notes for sites with detailed bird survey data, the authors created a transect of 70 sites through the California Coast Range from the Oregon border to northern San Luis Obispo County (Figure 1, Table 1). The transect spanned approximately 1,000 km north to south.

The resurveys were conducted at natural and semi-rural sites that experienced varying levels of both climate and land use change along coastal California. Minimum temperatures changed little over the past 50 years in northern portion of the study area (Del Norte, Siskiyou, Humboldt, Mendocino and northern portions of Sonoma Counties), while the southern portion (San Luis Obispo, Monterey, Santa Cruz, San Mateo, Santa Clara and Alameda Counties) had increasing minimum temperature ranging from 2-8 C° (LaDochy et al. 2007). Trends in mean and maximum temperature were more variable throughout this region, indicating areas of warming, little change, and even cooling, and suggest mean monthly temperatures may have warmed more in the north than in the south (LaDochy et al. 2007, Bonfils et al. 2008). During the 70 to 99 years since the original surveys, the 70 resurvey sites on average experienced an increase in both mean annual temperature and annual precipitation (see Methods for details). The research team avoided resurveying sites that experienced heavy land use change.

The study's goals were to: (1) produce an unbiased, longitudinal dataset of bird occupancy through strategic resurveys of avian diversity at sites with variable climate-change histories sampled by Grinnell and colleagues 70 to 99 years prior to the resurvey; (2) produce unbiased, spatially explicit occupancy estimates for 70-100 bird species using occupancy modeling to account for unequal detection probabilities of each species between sites, between the historic and modern eras, and between observers (MacKenzie et al. 2003, Tingley and Beissinger 2009); and (3) rank the ability of various climate change metrics and land use factors to explain changes in California bird distribution patterns over the past century.

The authors predicted bird turnover to be highest at sites that experienced the most climate change, at sites that experienced the most land use change, or both. In response to climate warming, species' ranges were predicted to shift northward, upslope, or toward the coast where the ocean may help to buffer changes in climate (but see Johnstone and Dawson 2010).

However, unless range shifts were dramatic, shifts associated with the latter predictions would probably be detectable only at range edges.

1.2. Methods

1.2.1. Mining Historic Data

The surveys conducted by Grinnell and colleagues were unusually well documented via: (1) field notes primarily housed at the University of California's Museum of Vertebrate Zoology, which document daily lists of species encountered at sites and sometimes include details of counts of bird species seen during timed bird walks; (2) the geo-referenced MVZ specimen database; and (3) images of sampling sites, which are web-accessible (mvz.berkeley.edu/FieldnotePhotoMap_Collection.html).

The MVZ field notes provided four essential kinds of information that allowed the research team to compile a quantitative record of Grinnell's work for analysis and comparison with the authors' contemporary surveys: (1) Local habitat descriptions which, in conjunction with locale information in the field notes, permitted spatial assignment of sampling locations (i.e., georeferencing) with high resolution; (2) Quantitative, repeated daily surveys for birds that allow us to reassemble the species encountered by Grinnell field workers on a day-by-day basis for use in occupancy models described below; (3) Quantitative records of the numbers of each bird species observed over a specified time period (i.e., timed area counts); and (4) Specimens that provided immutable proof of occupancy or presence-only information. The first two categories of information provided the core historic dataset that the research team assembled; the dataset was complemented by the third category of information when available.

In addition to the field notes housed at the MVZ, the authors mined the field notes housed at the Hastings Biological Field Station of the University of California Natural Reserve System (Hastings) and at the California Academy of Sciences in San Francisco (CAS). At Hastings the authors found the field notes of Jean Linsdale and Laidlaw Williams. Linsdale contributed extensive repeat surveys at Hastings and Williams contributed surveys at one site, a local state park. At CAS the authors found breeding bird survey data collected by Joseph Mailliard, the curator of birds at CAS, and a friend and colleague of Grinnell. Among Mailliard's bird survey data that the authors used were his notes associated with his publication on birds in the California Coast Range (Mailliard 1919).

A "bird survey" in the historic sense consisted of a variety of three different types of observations. The primary method of bird surveys conducted in the California Coast Range occurred as daily species lists recorded in their field notes. Grinnell and colleagues would take a hike or work a trap line, making note of all bird species seen or heard each day. This daily species list would usually contain additional annotations about habitat, location, time of day, etc. The second method of bird surveys was the "pencil census", a methodology pioneered by Grinnell and for which modern line transects are the most direct corollary. A pencil census consisted of an observer walking a trail or route, and tallying the number of each bird species observed, often divided into 1-hour increments. The third method is similar to the first: a complete list of the detected birds was recorded on day one; however, only new species were

recorded during subsequent survey days. The removal design (MacKenzie et al. 2006) is the most direct corollary to this method. The authors were able to use this type of historic survey by allowing the number of repeat visits at a site to vary by species. For example, if a species was detected on day 1 at a site, then it would not be recorded on subsequent days at that site. Therefore, only one survey would have been conducted for the species at that site. However, if a species was not detected until day 2, then the research team assigned it to have had two surveys: it was not detected on day 1 but was detected on day 2. The same line of logic continues for each subsequent day of the removal survey methodology conducted at a site.

For each potential site, the research team identified relevant records with the following information: observer, date, location, observation effort, numbers of observations by species, and local habitat. From this database, the authors tabulated detection/nondetection histories for each species at each site as required for the occupancy analyses (see below).

1.2.2. Site Selection

Within the resurvey area the authors revisited 70 sites surveyed for breeding birds in the early 1900's. The 70 sites were located in 20 counties of the California Coast Range (Figure 1, Table 1). The authors prioritized sites for resurvey that were historically surveyed on multiple occasions during the breeding season from approximately April 15 through July 15. However, 25 of the sites were surveyed fewer than 3 times in the historic era (14 were surveyed only once and 11 twice). Forty-six sites were historically surveyed 3 or more times, including one site which was surveyed 26 times.

Survey effort differed by era. Across the 70 sites more historic surveys (347) were completed than were modern surveys (216). Data were collected by 19 historic surveyors and 5 modern surveyors (Table 2). Historic surveys were composed of 253 complete daily bird lists, 52 "pencil censuses" of which 49 were done by Grinnell, and 48 daily lists of the new birds seen (i.e., removal surveys) of which 40 were conducted by Mailliard.

1.2.3. Bird Resurveys

Systematic bird inventories were conducted using variable-distance, seven-minute point counts during the breeding season, which has been the standard bird survey method used in the Grinnell Resurvey Project. Point count transects allow the use of both occupancy modeling (MacKenzie et al. 2003) and distance sampling (Thomas et al. 2010). Resurveys were completed during breeding seasons (April-June) in 2009 and 2010, and where feasible, resurvey dates were chosen to match the original surveys at each site.

Resurveys consisted of 2 to 3 km transects, each with 10 ($n = 64$) or 11 ($n = 6$) point count stations typically spaced 200-300 m apart. Transects spanned local vegetation heterogeneity and were located to best sample the areas surveyed by Grinnell and colleagues as described in their field notes and maps. The location of each station was determined with a GPS unit. The average elevation of the 70 sites was 525m (range = 0-1808m).

After arriving at a sample point on the transect, the observer waited for 60 seconds and then conducted a 7-minute point count, noting each bird seen or heard. For each individual detected,

the research team recorded species code, number of individuals in the group, how identified (singing, calling, visual), whether the bird was flying over, any observed breeding behavior, and the estimated distance from the observer to the bird using a laser range finder. Survey transects were visited three ($n = 64$) or four ($n = 6$) times within a single season, typically on consecutive days. When possible, repeat surveys at a site were conducted by different observers ($n = 17$). Due to logistical constraints the same observer generally conducted all surveys at a site ($n = 53$). Repeat visits allow the calculation of probabilities of detection and occurrence (MacKenzie et al. 2003).

1.2.4. Occupancy Modeling

The research team used single-species, multi-season occupancy models (MacKenzie et al. 2003) to analyze patterns of distribution and the potential mechanisms underlying site occupancy dynamics for 100 bird species, primarily passerines, that were detected in at least 10 percent of the 70 sites in either of the two eras. Detection histories at sites sampled in the historic, Grinnell era were modeled as season one, and those from the modern era were modeled as season two. Using this modeling framework the research team estimated each species' probability of occupancy during the historic (ψ_1) and modern (ψ_2) eras, and its probabilities of colonization (γ ; probability that a species was absent historically at a site but present during resurveys), extinction (ϵ ; probability that a species was present historically at a site but absent during resurveys), and detection (p). Multi-season occupancy models were performed using the RMark package in program R version 2.12.2 (R Development Core Team 2011).

The research team developed a set of candidate models to test the effects of climate change and land use change on the local colonization and extinction processes of the birds in the California Coast Range. A challenge the research team faced in using the multi-season occupancy models was limiting the model set to describe the four parameters (p , ψ , γ , and ϵ) without overdescribing the data. For each parameter, the research team included a constant probability model [i.e., $p(\cdot)$, $\psi(\cdot)$, $\gamma(\cdot)$, $\epsilon(\cdot)$], as well as models with predictor variables or covariates that may affect the parameter (Table 3).

The authors developed a candidate set of eight detectability (p) models to test four variables (observer, Julian date, Julian date \times Julian date, and era), the additive effects of variable combinations, and the constant $p(\cdot)$ model (Table 3). Twenty-four surveyors collected data across the historic and modern eras (Table 2). The research team simplified the modeling of observer by combining observers within era who conducted fewer than 20 complete surveys (excluding surveys that used a removal design). Thus, the research team modeled 9 observers (5 historic and 4 modern). As none of the observers collected data in both eras, the team did not use the additive effect of era and observer because these parameters were confounded. For any given species, only a subset of the 9 p models were among the top models (i.e., within 2 AICc points from the best model). Because each of the nine models performed best for some of the species, the research team retained all nine p models in the model set for each species. The authors also tested whether differences in timing of surveys between the two eras affected the probability of detection. The authors did this by including the interaction of era \times Julian date and era \times Julian date \times Julian date. These models generally did not perform as well as the others.

Moreover, there was as much if not more variation in seasonality within an era as between eras. For example, the breeding season occurred much later in 2010, which was a wet year with late winter storms, than in 2009. The historic era was likely to have even more seasonal variation between years simply because it spanned more years. By summing the AICc weights of the p models across all species, the authors assessed the relative importance of each variable or variable combination to species detection (Burnham & Anderson 2002).

The model set for initial (i.e., historic) occupancy consisted of six Psi (ψ) models. Occupancy covariates included elevation, latitude, historic climate (mean annual temperature, mean precipitation, and their additive effect) and the $\psi(\cdot)$ model. Historic climate variables were decadal averages (1900-1939) derived from WorldClim climate layers (Hijmans et al. 2005).

The authors tested seven variables and variable combinations for Gamma (γ) and Epsilon (ϵ) parameters, in addition to the $\gamma(\cdot)$ and $\epsilon(\cdot)$ models, to determine which factors were most associated with colonization and extinction probabilities (Table 3). Predictor variables consisted of the changes in mean annual temperature and in mean precipitation between eras derived from the Hijmans et al. (2005) WorldClim climate layers, a human influence index that described modern land use intensity (Sanderson et al. 2002), and their additive effects. The value of each variable associated with a site was calculated as the average value within a 1km buffer around each survey point within each site. The authors estimated the change in climate between the modern and historic eras by subtracting the historic (1900-1939) mean decadal averages from the modern (1970-2009) mean decadal averages. Of the 70 sites, 65 experienced warming from the historic to modern era and the other 5 cooled (Figure 2A). The mean annual temperature across the 70 sites increased by an average of 0.29°C (range = -0.24 to 0.82°C). A concentrated temperature increase can be seen in the San Francisco Bay Area. Only six of the 70 sites experienced less precipitation in the modern era than in the historic era (Figure 2B). Across sites, the change in annual precipitation increased on average by 4.59mm (range = -16.76 to 23.85mm).

Using all variable combinations across the four types of parameters would have resulted in a model set with nearly 3,500 models and overdescribed the data. Therefore, the authors limited their a priori model set for each species to 324 γ models and 324 ϵ models (Table 4). The authors arrived at this reduced model set by using all combinations of p models and ψ models, but not with all combinations of γ and ϵ models. While the authors crossed $\psi(\cdot)$, $\psi(\text{elevation})$, and $\psi(\text{latitude})$ with each γ and ϵ parameter, they only combined the climate variables in ψ with non-climate variables (e.g., the human influence index) in γ or ϵ or with the same climate variables in γ or ϵ . For example, if historic temperature was included in ψ , then the only climate variable included in γ or ϵ would have been the difference between the modern and historic temperature and/or the human influence index, but not the difference between the modern and historic precipitation. Similarly, the authors limited combinations to the additive effect of climate variables in ψ with non-climate variables and with the additive effect of climate variables in γ or ϵ . Furthermore, the authors independently modeled γ and ϵ , such that models with γ covariates were only run together with the constant probability ϵ model, and vice versa (Table 4).

Reliable historic metrics of vegetation, habitat, human influence, or land use appropriate for the study area are not available, so the authors were not able to calculate a metric of habitat change for their sites. Instead the authors used an index of human influence (Sanderson et al. 2002). This index included population density, land cover and land use, electric power infrastructure, and accessibility from road, rivers and coastlines. Although estimated using data circa 1995, the authors assumed the index is representative of the degree of land use change between the historic and modern eras, and the authors refer to this index as a metric of land use change. The authors scaled the index to range from low (0) to high (1). The average human influence index value across the 70 sites was 0.29 (range = 0.06 to 0.76). Sites with relatively high index values were assumed to have experienced more land use change (Figure 2C). Most of this change likely occurred in the years between the historic surveys and modern surveys. The San Francisco Bay Area had a concentration of sites with relatively higher land use intensity than elsewhere. The authors further resolved the problem of the lack of a historic land use metric by selecting sites that had undergone minimal land use and habitat change between the two eras; they selected resurvey sites whose modern habitat type matched that described in the historic field notes. It is important to note that the authors did not survey sites where native habitats had been converted to urban or industrial landscapes.

Not all species that were detected could be modeled. In order for a species to be modeled, it had to be detected a minimum of 10 percent of the 70 sites in either of the two eras. Furthermore, because this study focused on terrestrial birds, the authors limited their modeling efforts to terrestrial species—primarily passerines and near-passerines that breed within the study area. However, the authors did record all species detected, including shorebirds, seabirds, and waterfowl. A total of 220 species of birds were detected across the historic and modern surveys (Appendix 1). One hundred sixteen species that breed within the study area were detected at ≥ 10 percent of the sites in either survey era. Of these 116 species, the research team removed five nocturnal species and seven water birds from the model set because their survey methodology was not designed for detection of these species. The research team also removed four species from further analysis because the full constant probability model [$p(\cdot) + \psi(\cdot) + \gamma(\cdot) + \varepsilon(\cdot)$] failed to converge for these species. Based on these criteria, the team modeled site occupancy dynamics for a total of 100 of the 220 species detected.

The authors identified the best set of models for each species via an information theoretic approach (i.e., Akaike's information criterion corrected for small sample size (AICc), Burnham and Anderson 2002). Models that failed to converge were removed from that species' model set. The authors used AICc to rank the models for each species, independently ranking models that described γ from those that described ε . To account for uncertainty in model selection, the authors calculated AICc model weights and identified the top γ models and the top ε models using a 95 percent confidence set (summed weights; Appendices 2 and 3).

To estimate the probability of occupancy for each survey period (ψ_1 = historic era, ψ_2 = modern era), the research team model-averaged ψ_1 and ψ_2 estimates from the 95 percent confidence sets for γ and ε . The change in the probability of occupancy between the two survey eras ($\psi_2 - \psi_1$) indicates how species' distributions have changed.

The research team ranked each variable's importance in affecting a species colonization and extinction dynamics. For each species, the team estimated the relative importance of variable x_j used in γ and ε by summing the weights across all models in the 95 percent confidence set where variable j (or $\gamma(\cdot)$ and $\varepsilon(\cdot)$) occurred, thereby generating a cumulative weight for each variable (Burnham and Anderson 2002). For each species, the research team scaled the cumulative weights to sum to one. If the scaled cumulative weight of a variable in the γ or ε parameters was larger than each of the other variables by more than 0.1, then the research team assigned that variable as having the most important effect in a species' colonization or extinction dynamics. The team considered the effects of multiple variables if all three predictor variables (change in annual mean temperature, change in annual precipitation, and land use intensity) were larger than the scaled cumulative weight of the constant probability models, or if at least two of the three predictor variables were more than 0.1 larger than the scaled cumulative weight of the constant probability models, or both. The research team determined the direction of each variable's effect by the sign of the model-averaged coefficients from the 95 percent confidence set. The team tested whether the number of species affected by predictor variables and variable groups differed between colonization and extinction dynamics using a χ^2 test. The team avoided the problem of low frequency groups associated with the χ^2 test by combining γ or ε groups that consisted of land use and one or both of the climate change variables.

The research team determined whether each variable was generally more likely to be positively or negatively associated with colonization and with extinction. For each species the team used the scaled cumulative weight associated with a specific variable and separately weighted the positive and negative effect directions. For example if the scaled cumulative weight of temperature change for a species was 0.3 and the species' colonization dynamics were positively associated with temperature, then the positive effect of temperature on that species' colonization would be 0.3 and the negative effect would be zero. The authors then summed the weighted direction of effects across all 100 species and calculated the proportion of each weighted direction of effect. The authors did this separately for each variable and for local colonization and extinction dynamics. Using unpaired, two-tailed t-tests the research team tested for significant differences between the weighted positive and negative associations with each variable across the 100 species. This required six t-tests, one for colonization and one for extinction dynamics associated with change in temperature, change in precipitation, and land use intensity, therefore, the team employed a Bonferroni correction, adjusting the standard 0.05 alpha value to $\alpha = 0.0083$.

The authors examined patterns of colonization and extinction dynamics for species groupings based on taxonomy (passerine, raptor, woodpecker, other), resident vs. nonresident passerine, foraging guild (insectivore, granivore, omnivore, other), nest type (cup, cavity, other), clutch size, and body mass. The authors tested whether the primary predictor(s) of colonization and extinction differed from random across species groups using χ^2 tests for each grouping. The authors tested colonization and extinction predictors separately. The authors avoided the

problem of low frequency groups associated with the χ^2 test by combining γ or ε groups that consisted of land use and one or both of the climate change variables.

To visualize occupancy dynamics across the historic and modern eras, the authors mapped the occupancy history for each species. Each of the 70 survey sites was assigned one of four occupancy categories: unoccupied (not detected in the historic or modern era), persistence (detected in both historic and modern eras), colonization (detected only in modern era), or extinction (detected only in historic era). The authors used the model-averaged probability of detection to estimate the confidence in their assignment of each species to an occupancy category (Table 5). The authors assumed that there were no false detections in either era; therefore, 100 percent confidence was assigned to sites that were occupied in both eras (i.e., persistence). Confidence that a site was unoccupied in both eras was estimated from the product of the probability of detection in the historic era times the probability of detection in the modern era. Confidence that a site was colonized in the modern era was estimated from the probability of detection in the historic era. Conversely, the confidence that a site went extinct in the modern era was estimated from the probability of detection in the modern era.

The authors used a multivariate linear regression to test the effect of land use change, climate change, and the environmental covariates on species turnover at a site. The authors calculated a single metric of species turnover for each site by summing the probability of colonization and extinction at that site across all 100 species. The probability was based on observed data and the estimated probability of detection (Table 5). The authors used a backward stepwise regression by AIC to select the best model that predicted turnover, and they evaluated variable significance. The full model included the site-specific differences between modern and historic mean annual temperature and annual precipitation, and the site's human influence index, elevation, latitude, and distance to the ocean, all regressed against the site-specific composite measure of species turnover.

1.3. Results

1.3.1. Species Detected

More bird species were detected in the modern era ($n = 199$) than in the historic era ($n = 174$). Of the 220 total species detected in the historic and modern surveys, 153 were detected in both eras (Appendix 1). All 100 species that the authors modeled were detected in the modern era. However, two species - the Red-shouldered Hawk and European Starling - were not detected at any sites in the historic era, but were detected at 30 and 28 sites, respectively, in the modern era. Apparent colonization and extinction of species at sites appeared to occur frequently (Appendix 4).

1.3.2. Factors Affecting the Probability of Detection

Model-averaged detection probabilities per species ($n = 100$) were significantly greater for modern ($\bar{x} = 0.65 \pm 0.02$, se) than historic ($\bar{x} = 0.34 \pm 0.02$, se) surveys (paired t-test, $t = 13.92$, $P \leq 0.001$). Detection probabilities were most influenced by differences among observers (which was confounded with era), followed by Julian date and era (Table 6). Because the historic probability

of detection was lower than the modern counterpart, the authors were less confident in the probability of a site becoming colonized than going extinct. Thus, the authors display site-level changes in species' distributions between eras weighted by the confidence in their site-level detection probabilities (Appendix 4).

1.3.3. Changes in the Probability of Occupancy Over a Century

Model-averaged estimates of occupancy (Appendix 5) changed little ($-0.1 < \Delta\psi < 0.1$) over a century for about half ($n = 53$) of the 100 bird species the authors modeled (mean = -0.03 ; Figure 3). For the other half, however, about twice as many species decreased ($n = 32$) in occupancy by > 0.1 as those that increased in occupancy by > 0.1 ($n = 15$). Anna's Hummingbird had the largest increase in the probability of occupancy by 0.6, while occupancy probabilities of five other species increased by > 0.25 (Common Raven, Red-Shouldered Hawk, European Starling, Brown-headed Cowbird, and Violet-green Swallow). Tree Swallows had the largest decrease in probability of occupancy (-0.4). Occupancy probabilities of nine other species decreased by > 0.25 (in order of greatest decrease: White-breasted Nuthatch, House Finch, Savannah Sparrow, Western Meadowlark, Downy Woodpecker, Red-tailed Hawk, Western Bluebird, American Kestrel, Black Phoebe, and Vaux's Swift). Additional species-specific occupancy results are discussed below, as they relate to the factors affecting local colonization and extinction.

1.3.4. Factors Associated With Sites of High Species Turnover

The author's single metric of species turnover was associated with change in mean annual temperature, latitude, and elevation, based on multivariate linear regression using AICc for model selection (Table 7). Species turnover increased significantly at sites with warming temperatures, higher latitudes, and lower elevations. The best-fitting model did not include site-level measures of land use, change in annual precipitation, or distance from the ocean.

1.3.5. Factors Affecting Species Probabilities of Local Colonization and Extinction

In general, local extinctions were more likely at sites that got hotter, local colonizations were more likely at sites that got wetter, and land use intensity did not have a strong effect on local colonization or extinction dynamics (Table 8). More specifically, when assessing the responses of 100 bird species to environmental change, there was no significant difference in the direction of effect that temperature change had on colonization dynamics. However, temperature change had a strong and significant effect on local extinctions at sites that warmed: extinctions were associated with increasing temperatures. The authors also found that species were significantly more likely to colonize sites that experienced an increase in precipitation, though extinction dynamics were not significantly affected by precipitation change. While more intensive land use change appeared to positively affect colonization and negatively affect extinction dynamics, this effect was not significant once the Bonferroni correction ($\alpha = 0.0083$) was applied (Table 8).

Multi-season occupancy models indicated the strength of predictor variables in explaining colonization and extinction dynamics varied by species (Table 9). Land use intensity, change in temperature, and change in precipitation, either singly or in combination, explained local colonization dynamics for 54 percent of the species and local extinction dynamics for 60 percent of the species, while turnover was unexplained (i.e., constant probability) for about one-third of

the species (Figure 4). Of those species whose turnover dynamics could be attributed to a factor, land use intensity accounted for 19 percent of the species' colonization or extinction dynamics. This was followed by land use and climate change together (12.5 percent of the species), temperature change (12 percent of the species), precipitation change (8 percent of the species), and finally the combination of temperature and precipitation change, which accounted for 5 percent of the species' colonization or extinction dynamics (Table 9). However, there were more species whose colonization or extinction dynamics were best explained by climate change (25.5 percent, i.e., the sum of the number of species best explained by the change in temperature, change in precipitation, or change in both) than by land use alone (19 percent). As expected, covariates of turnover had positive effects on colonization and extinction dynamics for some species and negative effects for others (Tables 10 and 11). Interestingly, the same factor was attributable to both colonization and extinction for only 8 species, although 15 species' colonization and extinction dynamics were both explained by the constant probability model. The distribution of species among predictor variables (Figure 4) did not differ between γ and ϵ models ($\chi^2 = 6.29$, $n = 7$, $df = 6$, $p = 0.39$; $n = 7$ because the authors combined the groups with both land use and climate variables).

Below the authors discuss each of the predictor variables in terms of the species whose colonization and extinction dynamics were most affected by it.

1.3.6. Land Use Intensity Effects on Turnover

Land use intensity, the authors' metric for habitat change, explained colonization probabilities for 17 species (Table 10), and extinction probabilities for 21 species (Table 11). Only five species had both colonization and extinction dynamics attributable primarily to land use intensity (Table 9). Chestnut-backed Chickadees and Turkey Vultures were more likely to colonize and less likely to go extinct at sites with increased land use intensity. In contrast, Yellow-rumped Warblers, House Wrens, and Western Bluebirds were less likely to colonize and more likely to go extinct at sites with more intensive land use.

The association of colonization with land use resulted in mixed changes in occupancy. Of the 17 species whose colonization dynamics were best explained by land use intensity, five were less likely and 12 were more likely to colonize a site as land use intensity increased. The probability of occupancy declined by ≥ 0.1 for three of these species (Western Bluebird, Purple Finch, House Wren), while none of the species whose colonization dynamics were negatively associated with land use increased occupancy probabilities by ≥ 0.1 . Three species with colonization probabilities positively associated with land use had a ≥ 0.1 increase in occupancy (Violet-green Swallow, Chestnut-backed Chickadee, Orange-crowned Warbler), whereas two species had a ≥ 0.1 decrease in occupancy (Black Phoebe, Cliff Swallow).

The association of extinction with land use also resulted in mixed changes in occupancy. For the 21 species whose extinction dynamics were best explained by land use intensity, eight species were more likely and 13 were less likely to experience local extinction with more intensive land use. Six of the eight species with extinction probabilities positively related to land use intensity

had a > 0.1 decrease in the probability of occupancy (Western Meadowlark, Western Bluebird, American Kestrel, Lawrence's Goldfinch, Red-winged Blackbird, and House Wren), whereas none had a ≥ 0.1 increase in occupancy. Three of the 13 species less likely to go locally extinct with increasing land use intensity also increased in occupancy by ≥ 0.1 (Red-breasted Nuthatch, Allen's Hummingbird, and Chestnut-backed Chickadee), whereas two species showed a ≥ 0.1 decrease in occupancy (Vaux's Swift and Band-tailed Pigeon) despite being less likely to experience local extinctions with increasing land use intensity.

1.3.7. Change in Temperature and its Effects on Turnover

Change in mean annual temperature accounted for the colonization dynamics of 13 species and the extinction dynamics of 11 species (i.e., the scaled cumulative weight of temperature change was greater than each of the other variables by more than 0.1; Tables 10 and 11). Both colonization and extinction were best explained by temperature change for two species: Belted Kingfisher and Olive-sided Flycatcher (Table 9). As sites warmed, the Belted Kingfisher was less likely to colonize and more likely to experience local extinctions. Warming had an opposite effect on the Olive-sided Flycatcher.

Colonization was positively associated with warming for five species and negatively associated with warming for eight species. Two of the five species that colonized warming sites had increased in occupancy by ≥ 0.1 (Spotted Towhee, Dark-eyed Junco), whereas one species decreased by ≥ 0.1 (Olive-sided Flycatcher). Three of the eight species that were less likely to colonize warming sites also decreased in occupancy by ≥ 0.1 (American Crow, American Kestrel, Tree Swallow). The probability of occupancy did not increase by ≥ 0.1 for any of the 8 species negatively associated with warming.

Local extinction was positively related with warming for nine of the 11 species whose extinction dynamics were best explained by a change in temperature. The probability of occupancy changed by ≥ 0.1 for two of these nine species: it increased for the Brown-headed Cowbird and decreased for the Lark Sparrow. One of the two species whose extinction dynamics were negatively related to temperature decreased in occupancy by ≥ 0.1 (Olive-sided Flycatcher).

1.3.8. Change in Precipitation and its Effects on Turnover

Change in annual precipitation accounted for the colonization dynamics of 10 species and the extinction dynamics of seven species (Tables 10 and 11). MacGillivray's Warbler was the only species whose colonization and extinction dynamics were both best explained by this metric; an increase in precipitation was positively associated with colonization and negatively associated with extinction.

Of the 10 species whose colonization dynamics were best explained by precipitation change, colonization was positively associated with increased precipitation for eight species and negatively associated with precipitation for two species. Three of the eight species that were

more likely to colonize sites as precipitation increased also showed a ≥ 0.1 change in their occupancy probabilities: occupancy of the Pacific-slope Flycatcher increased by ≥ 0.1 , whereas the Brewer's Blackbird and Vaux's Swift both decreased by ≥ 0.1 . Both species that were less likely to colonize sites where precipitation had increased also showed a ≥ 0.1 increase in the probability of occupancy (Common Raven, Allen's Hummingbird).

Local extinction was positively associated with increased precipitation for two species and negatively associated for five of the species whose extinction dynamics were best explained by change in annual precipitation. The two species more likely to experience local extinctions as sites got wetter also showed decreased in occupancy by ≥ 0.1 (Red-tailed Hawk, Common Yellowthroat). Four of the five species that were less likely to experience local extinctions with increasing temperature had a ≥ 0.1 change in their probability of occupancy: Winter Wrens and Black-throated Warblers increased, while Downy Woodpeckers and Black-headed Grosbeaks decreased.

1.3.9. Combined Effects of Climate Change on Turnover

There were three species whose local colonization dynamics were best explained by both mean annual temperature and annual precipitation (Table 10). Although, neither species showed a ≥ 0.1 change in the probability of occupancy, Dusky Flycatcher and Nuttall's Woodpecker were more likely to colonize sites that had experienced an increase in temperature and precipitation (Table 9). The occupancy probability of the Brown-headed Cowbird increased by ≥ 0.1 , and it was more likely to colonize sites that cooled and received more precipitation.

Both mean annual temperature and annual precipitation change were associated with extinction dynamics of seven species (Table 11). Five of these species were more likely to experience extinctions at sites that got hotter and wetter (Hammond's Flycatcher, Western Tanager, Loggerhead Shrike, Mountain Chickadee, and Western Kingbird), one species was less likely to go locally extinct as sites got warmer and wetter (Fox Sparrow), and one species was more likely to go extinct at sites that got hotter but less likely to go extinct at sites that got wetter (Chipping Sparrow). Of these seven species, only two showed a ≥ 0.1 change in their probability of occupancy (Hammond's Flycatchers increased and Chipping Sparrows decreased).

1.3.10. Combined Effects of Land Use Intensity and Climate Change on Turnover

There were 24 species whose turnover dynamics were associated with a dual effect stemming from land use intensity and the change in temperature, precipitation, or both (Tables 10 and 11). Colonization and extinction of the Northern Rough-winged Swallow were both explained by a combination of land use intensity and climate variables (Table 9). This species was more likely to colonize sites that underwent an increase in temperature and that had more intense land use. It was more likely to go extinct at sites where temperature and precipitation increased, and at sites with more intense land use. This species showed a small change in its occupancy probability (-0.02).

Eleven species had colonization dynamics associated with the combined effects of land use and climate change (Table 10). The Red-shouldered Hawk's probability of occupancy increased by ≥ 0.1 , with colonization positively associated with an increase in temperature and land use intensity. The probability of occupancy of Band-tailed Pigeons, Black-headed Grosbeaks, and Lazuli Buntings all decreased by ≥ 0.1 . Colonization dynamics of the first two species were best explained by the combined effects of land use, temperature, and precipitation, whereas land use and precipitation best explained colonization dynamics of the last species. The direction of effect of each variable differed by species (Table 10). Band-tailed Pigeons responded positively to land use and negatively to climate variables, Lazuli Buntings showed the opposite response, and Black-headed Grosbeaks were more likely to colonize a site with an increase in each.

The extinction dynamics of 14 species were best explained by a combination of land use and climate variables (Table 11). Seven of these 14 species increased in occupancy by ≥ 0.1 . The Common Raven, Pacific-slope Flycatcher, and Orange-crowned Warbler were less likely to go extinct as land use intensity increased. Common Ravens were also less likely to go extinct as precipitation increased. Pacific-slope Flycatchers showed this same trend, but in response to increasing temperatures instead of precipitation. Orange-crowned Warblers were more likely to go extinct as temperatures increased. The Tree Swallow, Savannah Sparrow, Pine Siskin, and Brewer's Blackbird had a ≥ 0.1 decrease in occupancy. While extinction dynamics of the first two species were related to a change in precipitation and land use, the directions of effects were in opposition. Tree Swallows were less likely to go extinct at sites that got wetter and had more intensive land use. Pine Siskins were less likely to experience extinctions as temperature and land-use intensity increased, but Brewer's Blackbirds showed an opposite trend and were less likely to go extinct as precipitation increased.

1.3.11. Turnover Unrelated to Climate or Land Use, or Unassigned

The constant probability model for γ and ϵ performed best for 34 and 29 of the 100 species, respectively (Tables 10 and 11). For these species, neither the climate nor land use variables explained occupancy dynamics. For 15 of these species, the constant probability model performed best for both γ and ϵ (Table 9).

Colonization and extinction dynamics were ambiguous for 12 and 11 species, respectively (Tables 10 and 11). For these species the authors could not unambiguously assign turnover to any of the tested variables, because the difference between the scaled cumulative weights of the constant probability model and one or more of the three predictor variables was less than 0.1. Two species, Swainson's Thrush and Yellow Warbler, had ambiguous dynamics for both colonization and extinction (Table 9).

1.3.12. Taxonomy and Life History Influences on Turnover

Factors affecting colonization and extinction dynamics were not significantly associated with species' taxonomy, foraging guild, or life history traits (Table 12). None of the species groupings had a distribution of primary predictors different than what would be expected at random for

either colonization or local extinction. Thus, there were no clear life history predictors of colonization or extinction dynamics.

1.4. Discussion

The 100 breeding bird species the researchers analyzed within the California Coast Range had individualistic colonization and extinction dynamics in relation to changing climate and land use intensity. Differences in species' biology resulted in varied responses to these forces of change. Although no single trend dominated local colonization and extinction patterns across all species, there were interesting trends that united seemingly disparate species and divided similar species. Fifty-seven percent of the local colonization and extinction dynamics were explained in relation to one or more of the three variables tested: land use intensity, change in mean annual temperature, and change in annual precipitation. Nearly 32 percent of the species' dynamics were most related to the constant probability model rather than any of the covariates. For some species cause for the observed dynamics could not unambiguously be assigned to any of these factors. Across all of the species analyzed, however, local colonizations were more likely at sites that got wetter and local extinctions were more likely at sites that got hotter, whereas land use intensity did not have as strong of a directional effect on the local colonization or extinction dynamics (Table 8).

Changes in mean annual temperature and annual precipitation, taken individually or in combination, explained 26 percent of the turnover dynamics, whereas land use intensity explained only 19 percent of the turnover dynamics. In addition, a combination of climate change and land use intensity explained 13 percent of the observed turnover dynamics. The direction of effect shown by each species in response to the variable that best described its colonization or extinction dynamics was sometimes counter to the authors' expectations, as discussed below.

The effects of both temperature and precipitation change can exacerbate or ameliorate conditions depending on the directions of change and the biology of a species. On average, species were more likely to go extinct at sites that got hotter and to colonize sites that on average got wetter. During the time interval between historic to modern surveys, most resurvey sites experienced warming and increased precipitation. The increase in precipitation at sites may have facilitated colonization and dampened the effect of extinctions associated with sites that got hotter.

Some changes in occupancy that occurred over the past century were supported by the Breeding Bird Survey data for California (Sauer et al. 2011). Both datasets found important increases or decreases in many of the same species. Yet, the research team found some species whose occupancy changed greatly in one direction that Sauer et al. (2011) found to have changed in the opposite direction. The methods of analysis and the spatial scales of study differed between this work and Sauer et al. (2011), and may not be strictly comparable.

1.4.1. Site-specific Turnover

Species turnover was greatest at sites that warmed and that were located at higher latitudes and at lower elevations. Turnover at higher latitudes may reflect changes in the species whose range limits are in the northern portion of the study area. Higher turnover at lower elevation may be associated with more intense land use and higher human population density at lower elevations, such as the San Francisco Bay Area. As land use intensity and climate change continue to increase in the future, their effects may well become more pronounced.

1.4.2. Species-specific Trends in Relation to Temperature Change

The Spotted Towhee and Dark-eyed Junco responded positively to the level of warming that occurred between the historic and modern surveys. The occupancy probabilities of both species increased by more than 0.1 and both were more likely to colonize sites that got hotter.

The Olive-sided Flycatcher was more likely to colonize and less likely to go extinct at sites that warmed. However, its probability of occupancy decreased between the historic and modern eras, a surprising finding given that most sites warmed and that it was favorably associated with warming. Sites that warmed may have served as attractive sinks for this species.

The most negative response associated with warming was a decrease in occupancy coupled with a propensity to either go extinct at sites that heated up or not to colonize them. Such species included Tree Swallows, American Kestrels, American Crows, and Lark Sparrows. The large decrease in the Tree Swallow's occupancy probability may have been partially due to competition with other cavity-nesting species including the European Starling and Violet-green Swallow (Brown et al 1992, Winkler et al. 2011). The interaction of competition and a negative response to warming may reduce occupancy and increase turnover rates.

Colonization dynamics of the Brown-headed Cowbird were negatively affected by temperature and positively affected by precipitation. This species was also more likely to go extinct as sites warmed. These somewhat confusing trends suggest that the Brown-headed cowbird responded negatively to a warming world unless an increase in precipitation helps to offset the negative consequences associated with warming. It seems unlikely that warming temperatures will directly reduce the cowbird's range given that this species had a large increase in occupancy, has recently spread across most of North America, is known to be associated with open habitats in a range of climates, and is a generalist nest parasite (Lowther 1993). Hosts are critical for cowbirds to successfully parasitize nests. Thus, if hosts species are adversely affected by climate change, then the nest parasite could also be adversely affected. Nevertheless, because the Brown-headed cowbird is a generalist in host selection, the authors expect it to continue to be successful, whether or not some of its hosts are adversely affected by climate change

1.4.3. Species-specific Trends in Relation to Precipitation Change

The extinction dynamics and increase in occupancy of the Black-throated Gray Warbler indicated that it responded positively to the precipitation increase that occurred between the two surveys. This species was less likely to go extinct at sites that got wetter. MacGillivray's Warbler showed a similar trend; its probability of occupancy increased by 0.9 because this

species was more likely to colonize and less likely to go extinct at sites with increased precipitation.

Species with reduced occupancy that were associated with wetter conditions included the Common Yellowthroat and Red-tailed Hawk. Both experienced a > 0.1 decrease in the probability of occupancy and were more likely to experience extinction at sites that got wetter. Colonization dynamics of these species were not clearly attributable to any factor.

1.4.4. Species-specific Trends in Relation to Land Use Intensity

As expected, many of the species that are tolerant of humans or facilitated by activities associated with humans showed a positive change in their modeled occupancy (e.g., Common Raven, Brown-headed cowbird, Anna's Hummingbird, European Starling). Thus, it was interesting that land use intensity did not better explain the colonization or extinction dynamics of these species. Rather, climate change covariates best described their dynamics. While these species are found in degraded habitats, including rural, residential and some urban areas, they are not restricted to these habitats.

For example, Common Ravens are associated not only with multiple habitats and climates, but also with humans in rural and sometimes urban areas (Boarman and Heinrich 1999). Nonetheless, the colonization dynamics of this species were positively associated with warming, while the probability of local extinction decreased primarily with increasing temperatures and secondarily with more intensive land use. Colonization dynamics of Brown-headed Cowbirds were negatively associated with warming and positively associated with precipitation increase, while constant probability models best predicted colonization and extinction dynamics of Anna's Hummingbird and European Starling. As a counter example, the American Robin has long been known to do well in association with moderate urbanization (Grinnell and Miller 1944) and the authors expected its colonization dynamics to be positively associated with land use. While colonization was positively and primarily associated with land use, it was also positively associated with increasing temperature and precipitation. Interestingly, the probability of occupancy for the American Robin increased by only 0.04 in the study area.

Land use intensity was relatively low at the survey sites. Even though some sites were adjacent to urban areas, the authors did not resurvey sites that had been urbanized or been subjected to wholesale habitat conversion from historic conditions. The authors intentionally resurveyed sites that had experienced minimal land use change in order to detect climate signals on occupancy. Thus, if a species responded positively to land use intensity, it did not necessarily mean that it responded positively to urbanization or habitat conversion. Sites with higher land use intensity may have had more edge or heterogeneous habitats. This type of habitat diversity may explain why some species were either more likely to colonize survey sites (e.g., Violet-green Swallows, Turkey Vultures, Cliff Swallows, California Quail, and Killdeer) or less likely to go extinct (e.g., Band-tailed Pigeons, Vaux's Swifts, Red-breasted Nuthatch, Hutton's Vireo, Song Sparrow, and White-throated Swift) at sites that had higher land use intensity. The positive association with land use intensity, as seen in Turkey Vultures, may be further

explained by roadkill supplementing their diet. The Cliff Swallow's positive association with land use intensity may have occurred because this species commonly builds nests under bridges or culverts, although occupancy of Cliff Swallows decreased between the two survey eras.

Not all human-tolerant or human-facilitated species increased in occupancy between surveys (e.g., Black Phoebe, House Finch). Perhaps some of these species have increased at locations that experienced a greater degree of habitat change than the authors included in this study.

Black Phoebe occupancy decreased by 0.25 from the historic to modern survey era. This was surprising because Black Phoebes are generally tolerant of humans. It is not uncommon for them to nest on human-made structures such as buildings and bridges, though they can be displaced by activities that destroy riparian habitat or divert water from otherwise suitable habitats (Wolf 1997). The survey sites were not subjected to this type of habitat change. In fact, the results show that this species' colonization dynamics were positively associated with land use intensity, but that its extinction dynamics were best described by the constant probability model. In other words, the predictor variables the authors used were not able to explain why Black Phoebe occupancy declined.

Despite the House Finch's recent range expansion from western to eastern North America and its association with both natural habitats and human-created habitats in rural and urban areas (Hill 1993), the constant probability model best explained local colonization and extinction dynamics within the study area. Furthermore, the data give evidence that this species has declined in the study area. This decline is consistent with North American Breeding Bird Survey data for California (Sauer et al. 2011). In California, disease (i.e., pox) is common and may lead to death, yet the cause of House Finch decline in the western U.S. is unknown (Hill 1993).

The occupancy probability of the American Crow declined by almost 0.20. Its colonization dynamics were negatively related to temperature increases, while its extinction dynamics could not be assigned to any of the variables tested. This species had been increasingly common until the arrival of West Nile Virus, a disease lethal to the severely susceptible American Crow. LaDeau et al. (2007) estimated West Nile Virus has reduced the American Crow population by 45 percent. West Nile Virus may be responsible for this bird's decrease in occupancy, which may explain why extinction had no relationship with any of the covariates the authors tested.

Western Bluebirds were negatively associated with land use intensity. It was less likely to colonize and more likely to go extinct at sites with increasing land use intensity. In California, the Western Bluebird has declined primarily due to loss of oak woodland habitat and the proliferation of a nonnative competitor for nest cavities, the European Starling (Zack et al. 2002). The results lend supporting evidence that in the California Coast Range, this species is no longer as widespread as it once was, with a 0.28 decrease in its probability of occupancy. In contrast, the Violet-green Swallow had a 0.25 increase in occupancy. Very little is known about the status of Violet-green Swallow populations (Brown et al. 1992), making this finding all the more interesting. Western Bluebirds and Violet-green Swallows are both cavity nesters and nest-site competitors. Violet-green Swallows are known to displace Western Bluebird from nests, even building nests over active Western Bluebird nests (Guinan et al. 2008). Although the

authors did not model the occupancy of bluebirds and swallows jointly using two-species occupancy models (Richmond et al. 2010) to determine their interactions, 10 of 17 sites where Western Bluebirds went extinct had either colonization by ($n = 6$) or persistence of ($n = 5$) Violet-green Swallows (Appendix 4). Nevertheless, local colonization dynamics of the two species were in opposition: Western Bluebirds were negatively associated and Violet-green Swallows were positively associated with land use intensity. Local extinctions of the Western Bluebird were best explained by increasing land use intensity, while models with no ϵ covariate relationship best explained local extinction dynamics of the Violet-green Swallow. Another cavity nesting species that uses similar habitat and whose occupancy also declined was the Tree Swallow. Colonization and extinction associations of this species were similar to those of the Violet-green Swallow. Moreover, 9 of 13 sites where Tree Swallows went extinct had either colonization by ($n = 5$) or persistence of ($n = 4$) Violet-green Swallows (Appendix 4). Thus, species interactions could play an important and unexplored role in changes that the authors observed.

Not all pairs of similar species with contrasting occupancy dynamics were the result of apparent species interactions. For example, the occupancy of Red-tailed Hawks decreased by 0.28, while occupancy of Red-shouldered Hawks increased by 0.46. It is not clear what drove these trends, as colonization and extinction dynamics were associated with different covariates for these species. Moreover, only 4 of 17 sites where Red-tailed Hawks went extinct had colonization by ($n = 2$) or persistence of ($n = 2$) Red-shouldered Hawks (Appendix 4).

Of the species whose local colonization and extinction trends were not modeled, there were some that showed patterns of increasing colonization that can generally be attributed to humans, whether directly or indirectly (Appendix 1). As might be expected, the number of sites where human-adapted and human-facilitated species were detected increased between the two survey eras. Humans have directly and positively affected Wild Turkey populations in California via introductions and releases. The number of sites with Wild Turkey detections increased dramatically, from no occupied sites in the historic era to 21 sites in the modern era. Although Wild Turkey introductions to the California mainland had started in the early 1900's, by 1944 this species was still not considered established (Grinnell and Miller 1944). Other exotics, whether intentionally released or not, have spread and are positively associated with humans (European Collared-dove and Rock Pigeon). Other species have been indirectly facilitated by humans via habitat modification (e.g., reservoirs attracting Bald Eagles and Ospreys; the creation of suitable habitat for Mallards and Canada Geese) and an increase in winter food (e.g., Canada Goose). Of these species, Mallards showed the largest, albeit naïve, increase from no occupied sites historically to 31 sites in the modern era. It is surprising that in the historic survey era, Mallards were never recorded; declines in this species had been noted by the first half of the 20th century, yet they were still a common species (Grinnell and Miller 1944). Data from the Breeding Bird Survey also show a significant increase in California's Mallards (Sauer et al. 2011).

1.4.5. Species' Range Shifts and Limitations of the Study

Range shifts, whether attributable to climate change or to other factors, are primarily expected to be detected along elevation gradients or at the edges of a species range. Although the study area covered an elevation range from sea level to 1800m, the elevation gradient was not large enough to expect much upslope movement in response to climate warming. Moreover, very few species that the authors analyzed have range limits within the California Coast Range study area (i.e., Vaux's Swift, Red-breasted Sapsucker, Nuttall's Woodpecker, Mountain Chickadee, Townsend's Solitaire, California Thrasher, Rufous-crowned Sparrow, Fox Sparrow, and Lawrence's Goldfinch). Of these, only the Mountain Chickadee appears to have shifted its range northward. Given these challenges, it is remarkable that the authors' analyses were able to associate many observed changes in bird distributions to the climate change covariates the authors tested.

Historic data of species distribution are incredibly valuable in understanding how and why distributions have changed and to project how they may be different in the future, but historic data often have limitations. Occupancy models helped overcome some limitations and ultimately provided an understanding of the mechanisms that best explained colonization and extinction events. This analytical framework yielded unbiased estimates of occupancy in the historic and modern eras, while accounting for unequal detection probabilities of each species between sites, between the historic and modern eras, and between observers. Historic survey methodologies were rarely consistent among surveyors, and sometimes were not consistent within a surveyor. The authors dealt with this inconsistency by requiring that historic data be associated with a single day (i.e., Grinnell's "pencil census" surveys and daily bird lists), and by modeling the effect of observer on detectability. Observer differences between the two eras may be attributable to several factors: survey methods used in the historic era were not standardized, surveyors were often multi-tasking (e.g., checking traps, using firearms to collect specimens, and noting birds), field guides were not widely available, and binoculars were of poorer quality compared to today's optics. To use the occupancy modeling framework, the authors ideally selected sites that had repeat surveys within era. Historically, however, 14 sites were only surveyed once. Fortunately 56 historic sites had multiple surveys to analyze data using occupancy models.

Another difficulty in working with this historic dataset was that historic vegetation and land use data were not available for the author's survey area. The authors addressed this issue by resurveying sites where these characteristics had not greatly changed, based on descriptions in the field notes. As historic geospatial data improves and the details of historic habitat conditions are quantified, inference from resurvey studies like this will be improved. For example, the biophysical settings layer in the landfire database provides maps of the probable dominant vegetation on the North American landscape prior to Euro-American settlement (www.landfire.gov/NationalProductDescriptions20.php).

1.5. Conclusion

Climate change is projected to continue at unprecedented rates in the coming years (IPCC 2007). Stralberg et al. (2009) projected that as a result of future climate change, bird communities will change in the study area, but less so than in other regions of California. Similarly, Jetz et al. (2007) projected that the effects of climate change and land use change on avian diversity will be less severe in California than in other places on Earth. Despite these predictions, the authors found a surprisingly large percentage of the 100 bird species analyzed to have already experienced local colonization and extinction dynamics attributable to climate effects (26 percent), land use effects (19 percent), or a combination of these factors (13 percent). Of the climate variables, more species' colonization and extinction dynamics were associated with change in mean annual temperature than change in annual precipitation, though both were relevant. Importantly, colonization was most likely at sites that got wetter and extinction was more likely at sites that got hotter. While the authors only sampled sites that had experienced relatively low levels of land use change, they expect that land use change to be an important driver of colonization and extinction dynamics at sites with greater land-use change, such as at sites where native habitat has been converted to agricultural or residential use.

Climate change may affect other aspects of avian biology in addition to the local probabilities of colonization and extinction that the authors examined here. Strong evidence exists that birds have shifted their migratory and breeding phenologies in response to a changing climate, and population declines in some species have been linked to climate change (Parmesan and Yohe 2003, Crick 2004). While species may be experiencing climate-related effects beyond those the authors examined and detected here, the heterogeneous topography in the California Coast Range may enable species to better cope with climate change by tracking their climatic niche as it shifts in space (Peterson 2003, Tingley et al. 2009).

Bird extinctions are expected to become more frequent as climate change and habitat loss and fragmentation continue (Şekercioğlu et al. 2004, Brook et al. 2008). Fortunately, none of the species historically detected in this study have gone extinct. However, birds in the study area generally had a lower probability of occupancy in the resurvey period than in the historic survey period. Indeed, most trends in local colonization and extinction were best explained by climate change and land use intensity. A continued decrease in local colonization rates and increase in local extinction rates may have similar consequences as those expected from species extinctions: a decrease in ecosystem services including decomposition, seed dispersal, pollination, and control of insect populations (Şekercioğlu et al. 2004).

With a better understanding of sensitivity of birds to climate change and land-use, wildlife managers and energy industry planners will effectively know which indicators to consider when planning for the preservation of birds and locating power generation facilities. Advanced planning for conservation areas will help energy providers site new facilities more quickly and economically, as well as decrease negative impacts on California's wildlife.

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Table 1. Site Information for Each of the 70 Avian Resurvey Sites That Comprised the Grinnell Resurvey Project in the California Coast Range, California, USA.

Latitude, longitude, and elevation values represent the transect center. See Figure 1 for map of sites with corresponding number.

Number	Site Name	County	Latitude	Longitude	Elevation, m
1	Patrick Creek	Del Norte	41.8793	-123.8490	298
2	Smith River	Del Norte	41.8565	-124.1180	15
3	Requa	Del Norte	41.5471	-124.0690	49
4	Head of Doggett Creek	Siskiyou	41.9042	-122.9260	1808
5	Mt Vernon Mine	Siskiyou	41.7251	-122.7410	1285
6	Yreka Creek	Siskiyou	41.6740	-122.7170	1193
7	Stewart Springs	Siskiyou	41.4160	-122.5080	1235
8	Near Callahan, Scott Valley	Siskiyou	41.3446	-122.8100	990
9	Delta	Shasta	40.8964	-122.3760	343
10	Wiregrass Prairie	Humboldt	41.1898	-123.8120	919
11	Coyote Peak	Humboldt	41.1295	-123.8550	935
12	Trinity River at Willow Creek	Humboldt	40.9468	-123.6200	136
13	Horse Mountain	Humboldt	40.8812	-123.7350	1364
14	Eel River, from Ferndale to mouth	Humboldt	40.6150	-124.2200	0
15	South Fork Mountain	Humboldt	40.6102	-123.5610	1760
16	Carlotta	Humboldt	40.5447	-124.0380	159
17	Little Van Duzen River	Humboldt	40.4870	-123.6270	731
18	South Fork Eel River, Richardson Grove SP	Humboldt	40.0203	-123.7880	209
19	Hayfork	Trinity	40.5515	-123.1720	713
20	Hastings Creek	Trinity	40.4862	-123.5330	756
21	South Fork Good's Creek	Trinity	40.3718	-123.0530	1094
22	Spiers Gulch	Trinity	40.3823	-123.0110	1092
23	Mad River	Trinity	40.1990	-123.2830	852
24	Clover Gulch	Trinity	40.1577	-123.2080	919
25	Round Valley, South of Covelo	Mendocino	39.7386	-123.2550	529
26	Hearst	Mendocino	39.4914	-123.2120	427

Number	Site Name	County	Latitude	Longitude	Elevation, m
27	Russian Gulch SP	Mendocino	39.3318	-123.7970	37
28	Big River SP	Mendocino	39.3058	-123.7790	41
29	Van Damme SP	Mendocino	39.2767	-123.7710	35
30	North Fork Gualala River	Mendocino	38.7773	-123.5030	35
31	Stony Creek at Winslow	Glenn	39.6103	-122.5230	256
32	Fouts Springs	Colusa	39.3485	-122.6900	797
33	North Side of Clear Lake, Pepperwood Grove	Lake	39.0541	-122.7750	576
34	Glenbrook	Lake	38.8572	-122.7740	718
35	Harbin Springs	Lake	38.7900	-122.6660	613
36	Rumsey, Arbuckle Road	Yolo	38.9035	-122.2510	269
37	Gualala Point	Sonoma	38.7535	-123.5120	24
38	South Fork Gualala River, headwaters	Sonoma	38.5374	-123.1800	321
39	Freestone	Sonoma	38.3722	-122.9280	153
40	Bodega Head and Salmon Creek	Sonoma	38.3340	-123.0630	28
41	Mt. St Helena, Robert Louis Stevenson SP	Napa	38.6572	-122.6120	995
42	Alamo Canyon, Gates Canyon Road	Solano	38.3913	-122.0630	327
43	Inverness Ridge	Marin	38.1090	-122.8900	104
44	Lagunitas Creek	Marin	38.0033	-122.6960	149
45	Phoenix Lake near San Anselmo	Marin	37.9618	-122.5810	147
46	Muir Woods	Marin	37.8980	-122.5830	134
47	Tennessee Valley	Marin	37.8518	-122.5440	41
48	Wildcat Canyon	Contra Costa	37.9049	-122.2500	339
49	Mt Diablo SP	Contra Costa	37.8777	-121.9220	949
50	Marsh Creek	Contra Costa	37.8653	-121.7530	118
51	Strawberry Canyon	Alameda	37.8714	-122.2370	279
52	Alameda Creek	Alameda	37.5415	-121.8540	115
53	Big Basin Redwood SP	Santa Cruz	37.1793	-122.2180	374
54	San Lorenzo River, Boulder Creek	Santa Cruz	37.1175	-122.1160	133

Number	Site Name	County	Latitude	Longitude	Elevation, m
55	Waddell Creek, Big Basin Redwood SP	Santa Cruz	37.1036	-122.2760	26
56	Point Lobos	Monterey	36.5164	-121.9450	25
57	Hastings Natural Reserve	Monterey	36.3835	-121.5540	552
58	Big Sur, Pfeiffer SP	Monterey	36.2496	-121.7830	109
59	Arroyo Secco	Monterey	36.2326	-121.4790	270
60	Junipero Serra Peak	Monterey	36.1540	-121.4230	1487
61	Salinas River near San Lucas	Monterey	36.1141	-121.0280	102
62	Chalk Peak	Monterey	35.9798	-121.4320	921
63	Panoche Pass	San Benito	36.6605	-121.1000	462
64	Bear Valley, Pinnacles National Monument	San Benito	36.5013	-121.1370	337
65	Pinnacles National Monument, east side	San Benito	36.4688	-121.1860	563
66	East Fork San Carlos Creek	San Benito	36.4388	-120.6550	575
67	San Benito Mountain	San Benito	36.3710	-120.6400	1493
68	Laguna Ranch	San Benito	36.3565	-120.8420	933
69	Santa Margarita	San Luis Obispo	35.3801	-120.6150	320
70	Between Pozo and La Panza summits	San Luis Obispo	35.3532	-120.2730	629

Table 2. Historic and Modern Observers who Conducted Surveys and Their Survey Effort. Effort is described by the number of sites surveyed, the number of complete surveys conducted (i.e., daily surveys with a record of all birds detected, pencil censuses, or standardized modern surveys), and the number of removal design surveys (i.e., daily surveys in which only newly detected species were recorded).

Surveyor	Era	Number of sites surveyed	Number of complete surveys	Number of removal design surveys
Grinnell, Joseph	historic	38	103	0
Taylor, Walter	historic	12	50	0
Linsdale, Jean	historic	3	35	0
Storer, Tracy	historic	4	25	0
Palmer, Fletcher	historic	4	15	6
Shelton, Alfred	historic	7	13	0
White, Halstead	historic	5	13	0
Mailliard, Joseph	historic	12	12	39
Rodgers, Thomas	historic	2	7	0
Sibley, Charles	historic	4	6	0
Wythe, Margaret	historic	4	5	0
Hunt, Richard	historic	4	4	2
Kellogg, Louise	historic	1	3	0
Gilmore, Raymond	historic	2	2	0
Swarth, Harry	historic	1	2	0
Williams, Laidlaw	historic	1	2	0
Behle, William	historic	1	1	0
Camp, Charles	historic	1	1	0
Johnson, David	historic	1	1	0
Epanchin, Peter	modern	31	74	0
Liu, Leonard	modern	19	55	0

Bosler, Justin	modern	22	54	0
Wu, Joanna	modern	11	18	0
Garcia, Dawn	modern	5	15	0

Table 3. Covariates Used to Model Detectability (p), Occupancy (Ψ), Colonization (Γ), and Extinction (ϵ). Historic (h) climate variables were used in Ψ . The difference (Δ) between the modern and historic climate variables were used in Γ and ϵ .

p variables	Ψ variables	Γ variables	ϵ variables
$p(\cdot)$	$\psi(\cdot)$	$\gamma(\cdot)$	$\epsilon(\cdot)$
$p(\text{era})$	$\psi(\text{elevation})$	$\gamma(\Delta\text{temp})$	$\epsilon(\Delta\text{temp})$
$p(\text{observer})$	$\psi(\text{latitude})$	$\gamma(\Delta\text{precip})$	$\epsilon(\Delta\text{precip})$
$p(\text{date})$	$\psi(\text{hTemp})$	$\gamma(\text{land use intensity})$	$\epsilon(\text{land use intensity})$
$p(\text{date} + \text{date}^2)$	$\psi(\text{hPrecip})$	$\gamma(\Delta\text{temp} + \Delta\text{precip})$	$\epsilon(\Delta\text{temp} + \Delta\text{precip})$
$p(\text{era} + \text{date})$	$\psi(\text{hTemp} + \text{hPrecip})$	$\gamma(\Delta\text{temp} + \text{land use intensity})$	$\epsilon(\Delta\text{temp} + \text{land use intensity})$
$p(\text{era} + \text{date} + \text{date}^2)$		$\gamma(\Delta\text{precip} + \text{land use intensity})$	$\epsilon(\Delta\text{precip} + \text{land use intensity})$
$p(\text{observer} + \text{date})$		$\gamma(\Delta\text{temp} + \Delta\text{precip} + \text{land use intensity})$	$\epsilon(\Delta\text{temp} + \Delta\text{precip} + \text{land use intensity})$
$p(\text{observer} + \text{date} + \text{date}^2)$			

Table 4. The 36 Combinations of Initial Occupancy (ψ), Colonization (γ), and Extinction (ϵ) That Were Used With Each of 9 Detection Models (p) to Create a Model Set That Was Run for Each Species Consisting of 324 Models. The 36 models listed here illustrate combinations where detection and extinction were held constant [$p(\cdot)$, $\epsilon(\cdot)$]. The authors independently modeled γ and ϵ , such that models with γ covariates were only run together with the constant probability of ϵ , and vice versa. To create the full set of 324 models, the constant detection probability parameter, $p(\cdot)$, in the models below was replaced with each of the eight other detection covariates and covariate combinations.

The 36 combinations of ψ , γ , and ϵ , illustrated with the $p(\cdot)$ model

$p(\cdot) + \psi(\cdot) + \gamma(\cdot) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\cdot) + \gamma(\Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\cdot) + \gamma(\Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\cdot) + \gamma(\text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\cdot) + \gamma(\text{land use intensity} + \Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\cdot) + \gamma(\text{land use intensity} + \Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\cdot) + \gamma(\Delta\text{temp} + \Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\cdot) + \gamma(\Delta\text{temp} + \Delta\text{precip} + \text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\cdot) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\text{land use intensity} + \Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\text{land use intensity} + \Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\Delta\text{temp} + \Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{latitude}) + \gamma(\Delta\text{temp} + \Delta\text{precip} + \text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\cdot) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\text{land use intensity} + \Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\text{land use intensity} + \Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\Delta\text{temp} + \Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{elevation}) + \gamma(\Delta\text{temp} + \Delta\text{precip} + \text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hTemp}) + \gamma(\cdot) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hTemp}) + \gamma(\Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hTemp}) + \gamma(\text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hTemp}) + \gamma(\text{land use intensity} + \Delta\text{temp}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hPrecip}) + \gamma(\cdot) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hPrecip}) + \gamma(\Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hPrecip}) + \gamma(\text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hPrecip}) + \gamma(\text{land use intensity} + \Delta\text{precip}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hTemp} + \text{hPrecip}) + \gamma(\cdot) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hTemp} + \text{hPrecip}) + \gamma(\text{land use intensity}) + \epsilon(\cdot)$
 $p(\cdot) + \psi(\text{hTemp} + \text{hPrecip}) + \gamma(\Delta\text{temp} + \Delta\text{precip}) + \epsilon(\cdot)$

$$p(.) + \psi(hTemp + hPrecip) + \gamma(\Delta temp + \Delta precip + \text{land use intensity}) + \varepsilon(.)$$

Table 5. Inference About Occupancy Dynamics and Turnover of a Species at a Site Based on its Naïve Site Occupancy History (1 = present and 0 = absent) for two eras (historic = h and modern = m) derived from its probability of detection (D), assuming no false positives. The probability of turnover for a site is the sum of the probabilities of colonization and extinction.

Occupancy history	Persistence (1,1)	Colonization (0,1)	Extinction (1,0)	Unoccupied (0,0)
1,1	1	0	0	0
0,1	$1-D_h$	D_h	0	0
1,0	$1-D_m$	0	D_m	0
0,0	$(1-D_h)*(1-D_m)$	$D_h*(1-D_m)$	$(1-D_h)*D_m$	$D_h D_m$

Table 6. The Set of Nine Detection (p) Models Tested and the Number of Species That Each Model Best Described Based on AICc Weights.

Detection Parameter	Number of Species
Observer	25
Observer + Julian date×Julian date	17
Observer + Julian date	17
Era	16
Era + Julian date	9
(.)	6
Era + Julian date×Julian date	6
Julian date×Julian date	3
Julian date	1

Table 7. Results of the Best-Fitting General-Linear Model Predicting Species Turnover (adjusted R² = 0.1). Turnover increased at sites that experienced the most warming, at higher latitude sites, and at lower elevation sites.

	Coefficient	<i>T</i>	<i>P</i>
Intercept	0.341	22.628	<0.001
Change in mean annual temperature	0.093	2.155	0.035
Latitude	0.020	2.087	0.041
Elevation	-0.018	-2.017	0.048

Table 8. Comparisons of the Direction of a Variable’s Effect on Local Colonization (γ) and Extinction (ϵ) Dynamics Based on Cumulative AICc Weights Across all 100 Species.

Significance between positive and negative associations with each variable was tested using six unpaired t-tests, one for each variable’s colonization and extinction parameters. The authors used a Bonferroni adjustment to correct for multiple tests; * indicates significance at $\alpha = 0.0083$.

Weighted proportions and test results	Δ temperature		Δ precipitation		land use intensity	
	γ	ϵ	γ	ϵ	γ	ϵ
Proportion of positive associations	0.49	0.63	0.66	0.48	0.59	0.39
Proportion of negative associations	0.51	0.37	0.34	0.52	0.41	0.61
P-value, unpaired, two-tailed t-test	0.80	0.003*	0.0005*	0.72	0.06	0.02
<i>t</i>	0.24	3.01	3.58	0.35	1.91	2.42

Table 9. The Relative Importance of Colonization (γ) and Extinction (ϵ) Covariates for the 100 Bird Species Modeled. Best-ranked covariates had cumulative AIC weights that were greater than other covariates by 0.1 in the models that account for the 95 percent confidence sets (see Methods).

	$\epsilon(.)$	$\epsilon(\Delta\text{temp})$	$\epsilon(\Delta\text{precip})$	$\epsilon(\text{land use})$	$\epsilon(\Delta\text{temp}+\Delta\text{precip})$	$\epsilon(\Delta\text{temp}+\text{land use})$	$\epsilon(\Delta\text{precip}+\text{land use})$	$\epsilon(\Delta\text{temp}+\Delta\text{precip}+\text{land use})$	$\epsilon, \text{ unassigned}$	$\gamma, \text{ Total}$
$\gamma(.)$	15	1	2	8	4	1	2	1	0	34
$\gamma(\Delta\text{temp})$	3	2	0	2	1	0	1	1	3	13
$\gamma(\Delta\text{precip})$	2	1	1	3	0	1	1	1	0	10
$\gamma(\text{land use})$	3	2	0	5	0	1	0	2	4	17
$\gamma(\Delta\text{temp}+\Delta\text{precip})$	1	1	0	1	0	0	0	0	0	3
$\gamma(\Delta\text{temp}+\text{land use})$	1	1	0	0	0	0	0	1	1	4
$\gamma(\Delta\text{precip}+\text{land use})$	1	1	0	0	0	0	0	0	0	2
$\gamma(\Delta\text{temp}+\Delta\text{precip}+\text{land use})$	0	1	1	2	0	0	0	0	1	5
$\gamma, \text{ unassigned}$	3	1	3	0	2	0	1	0	2	12
$\epsilon, \text{ Total}$	29	11	7	21	7	3	5	6	11	

Table 10. Occupancy Change ($\Delta \psi$) and Dominant Colonization (γ) Covariates for the 100 Bird Species Modeled Based on the Cumulative Weight of Covariates From Models in the 95 Percent Confidence Set. Species are ordered by the primary covariate associated with colonization and then by cumulative weight of that factor.

Species	$\Delta \psi$	Models in γ 95% set	1 ^o effect associated with γ	γ (.)	γ (Δ temp)	γ (Δ precip)	γ (land use)	Direction of effect, γ		
								Δ temp	Δ precip	land use
Red-breasted Sapsucker	0.01	12	γ (.)	0.88	0.04	0.03	0.04	-	+	+
Ash-throated Flycatcher	-0.01	10	γ (.)	0.80	0.17	0.03	0	+	+	NA
Northern Flicker	-0.04	20	γ (.)	0.71	0.02	0	0.27	-	NA	-
House Finch	-0.36	7	γ (.)	0.69	0.05	0.05	0.21	-	-	-
Townsend's Solitaire	0.00	13	γ (.)	0.68	0.11	0.02	0.19	+	-	-
Golden-crowned Kinglet	0.00	7	γ (.)	0.67	0.06	0.06	0.20	+	+	+
California Towhee	0.00	15	γ (.)	0.63	0.16	0.03	0.19	-	+	+
Loggerhead Shrike	0.00	20	γ (.)	0.61	0.05	0.13	0.21	-	-	-
Lawrence's Goldfinch	-0.24	15	γ (.)	0.61	0.08	0.18	0.13	+	+	-
Steller's Jay	0.01	31	γ (.)	0.61	0.04	0.16	0.19	+	+	+
Western Meadowlark	-0.34	39	γ (.)	0.60	0.16	0.09	0.15	-	+	-
Lark Sparrow	-0.22	34	γ (.)	0.59	0.12	0.10	0.20	-	+	+
European Starling	0.44	9	γ (.)	0.58	0.06	0.02	0.34	-	+	-
Hairy Woodpecker	-0.12	25	γ (.)	0.53	0.26	0.17	0.03	+	+	+
Bewick's Wren	0.00	7	γ (.)	0.52	0.19	0.19	0.10	+	-	-
White-throated Swift	0.00	45	γ (.)	0.51	0.05	0.20	0.24	+	+	+
Hammond's Flycatcher	0.10	26	γ (.)	0.51	0.16	0.03	0.29	-	+	-
Anna's Hummingbird	0.63	13	γ (.)	0.50	0.09	0.08	0.32	+	-	+
Black-throated Gray Warbler	0.13	33	γ (.)	0.49	0.22	0.13	0.16	-	-	+
Red-winged Blackbird	-0.21	27	γ (.)	0.47	0.17	0.17	0.19	+	+	+
Savannah Sparrow	-0.34	25	γ (.)	0.46	0.16	0.18	0.20	-	+	+
Acorn Woodpecker	0.00	17	γ (.)	0.44	0.27	0.01	0.27	+	+	+
Lesser Goldfinch	-0.14	12	γ (.)	0.44	0.29	0.12	0.15	+	+	-
Red-breasted Nuthatch	0.21	60	γ (.)	0.42	0.25	0.14	0.19	+	+	+
California Thrasher	-0.05	18	γ (.)	0.40	0.20	0.22	0.18	-	+	-

Species	$\Delta \psi$	Models in γ 95% set	1 ^o effect associated with γ	γ (.)	γ (Δ temp)	γ (Δ precip)	γ (land use)	Direction of effect, γ		
								Δ temp	Δ precip	land use
Fox Sparrow	0.00	91	γ (.)	0.40	0.22	0.15	0.23	+	+	-
Mountain Chickadee	-0.01	29	γ (.)	0.40	0.20	0.20	0.20	-	-	-
Song Sparrow	-0.03	32	γ (.)	0.39	0.19	0.23	0.18	+	+	+
White-breasted Nuthatch	-0.37	10	γ (.)	0.38	0.19	0.24	0.20	-	-	-
Western Scrub-jay	-0.09	25	γ (.)	0.37	0.20	0.23	0.20	+	+	-
Cassin's Vireo	-0.04	68	γ (.)	0.36	0.19	0.24	0.21	-	+	+
Wilson's Warbler	0.07	13	γ (.)	0.36	0.24	0.17	0.23	+	-	+
Downy Woodpecker	-0.31	20	γ (.)	0.35	0.22	0.22	0.21	-	+	-
Pine Siskin	-0.18	16	γ (.)	0.34	0.23	0.21	0.22	-	-	+
Olive-sided Flycatcher	-0.21	4	γ (Δ temp)	0	0.95	0.05	0	+	-	NA
Tree Swallow	-0.41	12	γ (Δ temp)	0.06	0.80	0.03	0.11	-	-	+
American Kestrel	-0.26	35	γ (Δ temp)	0.14	0.63	0.08	0.15	-	+	-
American Crow	-0.19	19	γ (Δ temp)	0.04	0.62	0.19	0.15	-	+	+
Rufous-crowned Sparrow	0.01	117	γ (Δ temp)	0.14	0.53	0.15	0.18	+	+	+
Western Kingbird	-0.06	28	γ (Δ temp)	0.19	0.53	0.16	0.12	-	+	-
Belted Kingfisher	-0.03	17	γ (Δ temp)	0.08	0.52	0.21	0.20	-	-	+
Spotted Towhee	0.22	57	γ (Δ temp)	0.01	0.50	0.32	0.17	+	-	-
Barn Swallow	0.01	29	γ (Δ temp)	0.16	0.48	0.18	0.18	-	-	-
Dark-eyed Junco	0.16	116	γ (Δ temp)	0.21	0.48	0.14	0.17	+	+	-
Bullock's Oriole	0.02	20	γ (Δ temp)	0.18	0.47	0.09	0.26	-	+	-
Bushtit	-0.08	30	γ (Δ temp)	0.04	0.43	0.23	0.30	-	-	-
Mourning Dove	-0.04	26	γ (Δ temp)	0.26	0.43	0.09	0.22	+	+	+
Purple Martin	-0.04	114	γ (Δ precip)	0.10	0.16	0.53	0.20	+	+	+
Warbling Vireo	0.06	50	γ (Δ precip)	0.09	0.25	0.51	0.16	+	+	+
Common Raven	0.53	65	γ (Δ precip)	0.11	0.21	0.50	0.18	-	-	+
Vaux's Swift	-0.25	62	γ (Δ precip)	0.10	0.20	0.47	0.22	+	+	+
Allen's Hummingbird	0.20	42	γ (Δ precip)	0.06	0.29	0.47	0.19	+	-	+
MacGillivray's Warbler	0.09	73	γ (Δ precip)	0.20	0.14	0.47	0.19	+	+	+

Species	$\Delta \psi$	Models in γ 95% set	1 ^o effect associated with γ	γ (.)	γ (Δ temp)	γ (Δ precip)	γ (land use)	Direction of effect, γ		
								Δ temp	Δ precip	land use
Pileated Woodpecker	0.01	26	$\gamma(\Delta$ precip)	0.02	0.30	0.43	0.24	+	+	+
Mountain Quail	-0.04	36	$\gamma(\Delta$ precip)	0.17	0.15	0.43	0.25	-	+	-
Brewer's Blackbird	-0.23	54	$\gamma(\Delta$ precip)	0.17	0.26	0.38	0.18	-	+	-
Pacific-slope Flycatcher	0.13	48	$\gamma(\Delta$ precip)	0.23	0.23	0.36	0.18	+	+	+
Violet-green Swallow	0.25	22	γ (land use)	0	0.09	0.09	0.83	-	-	+
Oak Titmouse	-0.02	6	γ (land use)	0.00	0.16	0.09	0.75	+	+	-
Purple Finch	-0.15	34	γ (land use)	0.12	0.06	0.11	0.71	+	+	-
Turkey Vulture	-0.05	22	γ (land use)	0	0.19	0.10	0.71	+	+	+
Cliff Swallow	-0.16	24	γ (land use)	0.01	0.17	0.17	0.66	-	+	+
House Wren	-0.13	40	γ (land use)	0.12	0.18	0.12	0.57	-	+	-
American Goldfinch	0.09	15	γ (land use)	0	0.18	0.28	0.54	-	-	+
California Quail	-0.07	38	γ (land use)	0.17	0.20	0.14	0.49	-	+	+
Western Bluebird	-0.28	50	γ (land use)	0.20	0.18	0.14	0.48	-	-	-
Killdeer	0.06	61	γ (land use)	0.28	0.13	0.13	0.47	-	+	+
Yellow-breasted Chat	-0.09	75	γ (land use)	0.05	0.17	0.33	0.45	-	+	+
Cooper's Hawk	-0.04	101	γ (land use)	0.17	0.14	0.25	0.44	-	+	+
Orange-crowned Warbler	0.10	46	γ (land use)	0.16	0.29	0.12	0.43	-	-	+
White-crowned Sparrow	-0.06	13	γ (land use)	0.02	0.32	0.24	0.42	-	+	+
Black Phoebe	-0.25	24	γ (land use)	0.22	0.29	0.08	0.40	+	-	+
Yellow-rumped Warbler	0.09	54	γ (land use)	0.19	0.20	0.22	0.39	-	+	-
Chestnut-backed Chickadee	0.13	15	γ (land use)	0.24	0.20	0.19	0.37	+	-	+
Brown-headed Cowbird	0.30	2	γ (Δ temp + Δ precip)	0	0.50	0.50	0	-	+	NA
Nuttall's Woodpecker	-0.02	13	γ (Δ temp + Δ precip)	0.05	0.44	0.39	0.12	+	+	-
Dusky Flycatcher	0.08	64	γ (Δ temp + Δ precip)	0.15	0.38	0.31	0.17	+	+	-
Red-shouldered Hawk	0.46	20	$\gamma(\Delta$ temp + land use)	0	0.43	0.11	0.46	+	+	+
Pygmy Nuthatch	-0.03	61	$\gamma(\Delta$ temp + land use)	0.04	0.37	0.13	0.46	+	+	+
N. Rough-winged Swallow	-0.02	22	$\gamma(\Delta$ temp + land use)	0.14	0.31	0.21	0.33	+	+	+

Species	$\Delta \psi$	Models in γ 95% set	1 ^o effect associated with γ	γ (.)	γ (Δ temp)	γ (Δ precip)	γ (land use)	Direction of effect, γ		
								Δ temp	Δ precip	land use
Spotted Sandpiper	-0.02	56	$\gamma(\Delta$ temp + land use)	0.13	0.39	0.18	0.30	-	-	-
Nashville Warbler	0.09	36	γ (Δ precip + land use)	0.03	0.14	0.42	0.41	-	+	-
Lazuli Bunting	-0.17	9	γ (Δ precip + land use)	0	0.25	0.36	0.38	+	+	-
American Robin	0.04	40	$\gamma(\Delta$ temp+ Δ precip+land use)	0.03	0.33	0.26	0.39	+	+	+
Band-tailed Pigeon	-0.22	28	$\gamma(\Delta$ temp+ Δ precip+land use)	0.01	0.27	0.33	0.39	-	-	+
Hutton's Vireo	-0.07	25	$\gamma(\Delta$ temp+ Δ precip+land use)	0.01	0.33	0.32	0.34	-	-	+
Blue-gray Gnatcatcher	0.06	29	$\gamma(\Delta$ temp+ Δ precip+land use)	0.09	0.27	0.30	0.34	+	+	-
Black-headed Grosbeak	-0.20	66	$\gamma(\Delta$ temp+ Δ precip+land use)	0.01	0.31	0.36	0.32	+	+	+
Hermit Warbler	0.04	52	unassigned	0.44	0.14	0.07	0.34	-	-	-
Brown Creeper	-0.03	14	unassigned	0.37	0.13	0.06	0.44	-	-	+
Chipping Sparrow	-0.14	49	unassigned	0.35	0.21	0.26	0.18	+	-	-
Wrentit	-0.16	38	unassigned	0.34	0.26	0.13	0.26	-	-	-
Swainson's Thrush	-0.11	5	unassigned	0.33	0.19	0.28	0.20	+	-	+
Winter Wren	0.22	24	unassigned	0.33	0.29	0.17	0.21	+	+	+
Western Tanager	0.07	7	unassigned	0.30	0.26	0.26	0.18	+	+	-
Yellow Warbler	-0.12	172	unassigned	0.30	0.35	0.16	0.18	-	-	-
Red-tailed Hawk	-0.28	37	unassigned	0.29	0.27	0.27	0.16	-	-	-
Common Yellowthroat	-0.10	112	unassigned	0.29	0.23	0.21	0.27	+	-	+
Hermit Thrush	-0.03	90	unassigned	0.27	0.20	0.30	0.22	-	+	-
Western Wood-pewee	-0.13	8	unassigned	0.26	0.34	0.19	0.20	-	-	+

Table 11. Occupancy Change ($\Delta \psi$) and Dominant Extinction (ϵ) Covariates for the 100 Bird Species Modeled Based on the Cumulative Weight of Covariates from Models in the 95 Percent Confidence Set. Species are ordered by the primary covariate associated with extinction and then by cumulative weight of that factor.

Species	$\Delta \psi$	models in	1 ^o effect associated with ϵ	ϵ (.)	ϵ	ϵ	ϵ	ϵ	Direction of effect, ϵ
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	ε 95% set			(Δ temp)	(Δ precip)	(land use)	Δ temp	Δ precip	land use	
European Starling	0.44	9	ε (.)	0.86	0	0.02	0.12	NA	+	+
Red-breasted Sapsucker	0.01	15	ε (.)	0.83	0.09	0.05	0.03	+	-	-
Ash-throated Flycatcher	-0.01	9	ε (.)	0.81	0.19	0	0	+	NA	NA
Bewick's Wren	0.00	6	ε (.)	0.77	0.11	0.11	0.02	-	-	+
Townsend's Solitaire	0.00	13	ε (.)	0.70	0.08	0	0.22	-	NA	-
Northern Flicker	-0.04	19	ε (.)	0.68	0.04	0	0.28	+	NA	+
House Finch	-0.36	7	ε (.)	0.68	0.06	0.06	0.21	-	-	+
Nuttall's Woodpecker	-0.02	11	ε (.)	0.67	0.07	0.07	0.19	-	+	+
Golden-crowned Kinglet	0.00	7	ε (.)	0.67	0.06	0.06	0.20	-	-	-
Lesser Goldfinch	-0.14	13	ε (.)	0.63	0.19	0.04	0.13	-	-	+
Wrentit	-0.16	34	ε (.)	0.58	0.11	0.12	0.19	-	-	-
Hairy Woodpecker	-0.12	24	ε (.)	0.57	0.37	0.05	0.01	-	+	+
Rufous-crowned Sparrow	0.01	110	ε (.)	0.57	0.09	0.12	0.22	-	-	-
Violet-green Swallow	0.25	43	ε (.)	0.54	0.17	0.10	0.19	-	+	+
Acorn Woodpecker	0.00	16	ε (.)	0.54	0.17	0.01	0.28	-	-	+
Anna's Hummingbird	0.63	12	ε (.)	0.53	0.11	0.09	0.28	+	+	+
California Towhee	0.00	16	ε (.)	0.48	0.19	0.10	0.23	+	+	+
Dark-eyed Junco	0.16	112	ε (.)	0.48	0.18	0.14	0.20	-	-	-
Red-shouldered Hawk	0.46	37	ε (.)	0.46	0.19	0.19	0.16	+	+	+
Warbling Vireo	0.06	53	ε (.)	0.43	0.18	0.18	0.21	-	-	+
Western Scrub-jay	-0.09	26	ε (.)	0.43	0.21	0.12	0.24	+	-	+
Cliff Swallow	-0.16	32	ε (.)	0.43	0.20	0.19	0.18	-	-	+
Hermit Thrush	-0.03	86	ε (.)	0.43	0.17	0.17	0.23	-	+	-
Mountain Quail	-0.04	32	ε (.)	0.41	0.19	0.19	0.21	-	+	-
Lazuli Bunting	-0.17	26	ε (.)	0.41	0.25	0.11	0.22	+	-	-
Black Phoebe	-0.25	26	ε (.)	0.41	0.15	0.27	0.16	+	+	+
Barn Swallow	0.01	22	ε (.)	0.37	0.21	0.22	0.20	+	-	-
Western Wood-pewee	-0.13	9	ε (.)	0.36	0.23	0.19	0.22	+	+	-
White-breasted Nuthatch	-0.37	7	ε (.)	0.36	0.20	0.19	0.25	+	+	-

Species	$\Delta \psi$	models in ε 95% set	1 ^o effect associated with ε	ε (.)	ε (Δ temp)	ε (Δ precip)	ε (land use)	Direction of effect, ε		
								Δ temp	Δ precip	land use
Olive-sided Flycatcher	-0.21	11	ε (Δ temp)	0.03	0.77	0.07	0.12	-	+	-
Brown-headed Cowbird	0.30	19	ε (Δ temp)	0	0.59	0.25	0.16	+	-	-
Lark Sparrow	-0.22	23	ε (Δ temp)	0	0.54	0.32	0.14	+	+	+
Purple Martin	-0.04	92	ε (Δ temp)	0.01	0.54	0.17	0.28	+	-	-
California Quail	-0.07	21	ε (Δ temp)	0.20	0.50	0.17	0.13	+	-	-
Blue-gray Gnatcatcher	0.06	19	ε (Δ temp)	0.13	0.50	0.23	0.15	+	-	-
Nashville Warbler	0.09	37	ε (Δ temp)	0.07	0.49	0.19	0.25	+	-	-
Pygmy Nuthatch	-0.03	32	ε (Δ temp)	0	0.45	0.32	0.23	-	+	-
Belted Kingfisher	-0.03	20	ε (Δ temp)	0.05	0.43	0.19	0.33	+	-	-
Oak Titmouse	-0.02	9	ε (Δ temp)	0.17	0.38	0.21	0.24	+	+	+
Hermit Warbler	0.04	63	ε (Δ temp)	0.20	0.36	0.19	0.25	+	-	+
Black-headed Grosbeak	-0.20	7	ε (Δ precip)	0	0.26	0.69	0.05	+	-	-
Black-throated Gray Warbler	0.13	40	ε (Δ precip)	0.03	0.15	0.63	0.18	+	-	-
Winter Wren	0.22	22	ε (Δ precip)	0.05	0.15	0.62	0.19	-	-	-
Downy Woodpecker	-0.31	17	ε (Δ precip)	0.00	0.26	0.55	0.19	+	-	-
MacGillivray's Warbler	0.09	54	ε (Δ precip)	0.02	0.18	0.50	0.29	-	-	+
Common Yellowthroat	-0.10	98	ε (Δ precip)	0.02	0.31	0.50	0.17	-	+	+
Red-tailed Hawk	-0.28	38	ε (Δ precip)	0.34	0.10	0.45	0.10	+	+	+
Band-tailed Pigeon	-0.22	12	ε (land use)	0	0.20	0.06	0.74	-	+	-
Vaux's Swift	-0.25	38	ε (land use)	0	0.14	0.15	0.72	-	-	-
Western Meadowlark	-0.34	23	ε (land use)	0	0.18	0.12	0.70	+	-	+
Red-breasted Nuthatch	0.21	46	ε (land use)	0.04	0.16	0.12	0.68	+	+	-
Hutton's Vireo	-0.07	43	ε (land use)	0.10	0.19	0.06	0.65	+	+	-
American Kestrel	-0.26	24	ε (land use)	0.04	0.27	0.05	0.64	-	-	+
Song Sparrow	-0.03	24	ε (land use)	0.01	0.16	0.23	0.61	-	+	-
White-throated Swift	0.00	33	ε (land use)	0.05	0.10	0.24	0.61	+	-	-
Lawrence's Goldfinch	-0.24	13	ε (land use)	0.03	0.29	0.10	0.59	+	-	+
Dusky Flycatcher	0.08	54	ε (land use)	0.22	0.17	0.03	0.58	-	+	-

Species	$\Delta \psi$	models in ϵ 95% set	1 ^o effect associated with ϵ	ϵ (.)	ϵ (Δ temp)	ϵ (Δ precip)	ϵ (land use)	Direction of effect, ϵ		
								Δ temp	Δ precip	land use
Red-winged Blackbird	-0.21	21	ϵ (land use)	0.13	0.17	0.15	0.55	-	+	+
Chestnut-backed Chickadee	0.13	8	ϵ (land use)	0	0.39	0.06	0.55	+	+	-
Cassin's Vireo	-0.04	71	ϵ (land use)	0.04	0.26	0.17	0.54	+	-	+
Western Bluebird	-0.28	48	ϵ (land use)	0.13	0.15	0.19	0.53	+	+	+
House Wren	-0.13	43	ϵ (land use)	0.08	0.16	0.24	0.53	-	-	+
Wilson's Warbler	0.07	11	ϵ (land use)	0	0.15	0.35	0.50	-	+	-
Yellow-rumped Warbler	0.09	25	ϵ (land use)	0	0.26	0.25	0.49	-	+	+
Allen's Hummingbird	0.20	27	ϵ (land use)	0.01	0.35	0.15	0.49	+	-	-
Pileated Woodpecker	0.01	36	ϵ (land use)	0.02	0.12	0.37	0.49	-	+	-
Bullock's Oriole	0.02	20	ϵ (land use)	0.16	0.24	0.14	0.45	+	+	-
Turkey Vulture	-0.05	46	ϵ (land use)	0.33	0.17	0.06	0.43	+	-	-
Western Tanager	0.07	3	ϵ (Δ temp + Δ precip)	0	0.46	0.45	0.09	+	+	-
Hammond's Flycatcher	0.10	20	ϵ (Δ temp + Δ precip)	0.01	0.44	0.43	0.11	+	+	-
Mountain Chickadee	-0.01	12	ϵ (Δ temp + Δ precip)	0.00	0.44	0.44	0.11	+	+	-
Chipping Sparrow	-0.14	25	ϵ (Δ temp + Δ precip)	0	0.44	0.43	0.14	+	-	+
Loggerhead Shrike	0.00	7	ϵ (Δ temp + Δ precip)	0.00	0.44	0.45	0.11	+	+	+
Fox Sparrow	0.00	81	ϵ (Δ temp + Δ precip)	0.03	0.42	0.39	0.16	-	-	+
Western Kingbird	-0.06	28	ϵ (Δ temp + Δ precip)	0.20	0.34	0.34	0.13	+	+	-
Pine Siskin	-0.18	10	ϵ (Δ temp + land use)	0.06	0.48	0	0.47	-	NA	-
Pacific-slope Flycatcher	0.13	19	ϵ (Δ temp + land use)	0.00	0.39	0.14	0.47	-	-	-
Orange-crowned Warbler	0.10	42	ϵ (Δ temp + land use)	0.06	0.43	0.10	0.40	+	+	-
Brown Creeper	-0.03	9	ϵ (Δ precip + land use)	0.08	0.13	0.38	0.41	+	+	-
Tree Swallow	-0.41	33	ϵ (Δ precip + land use)	0.02	0.20	0.39	0.39	+	-	-
Common Raven	0.53	57	ϵ (Δ precip + land use)	0.02	0.15	0.45	0.38	-	-	-
Savannah Sparrow	-0.34	23	ϵ (Δ precip + land use)	0.18	0.15	0.32	0.34	-	+	+
California Thrasher	-0.05	20	ϵ (Δ precip + land use)	0.16	0.20	0.34	0.30	+	-	+
Bushtit	-0.08	42	ϵ (Δ temp+ Δ precip+land use)	0.09	0.28	0.29	0.35	-	-	+

Species	$\Delta \psi$	models in ϵ 95% set	1 ^o effect associated with ϵ	ϵ (.)	ϵ (Δ temp)	ϵ (Δ precip)	ϵ (land use)	Direction of effect, ϵ		
								Δ temp	Δ precip	land use
Brewer's Blackbird	-0.23	41	$\epsilon(\Delta$ temp+ Δ precip+land use)	0.05	0.36	0.26	0.33	+	-	+
American Goldfinch	0.09	22	$\epsilon(\Delta$ temp+ Δ precip+land use)	0.12	0.27	0.30	0.32	+	+	-
Steller's Jay	0.01	33	$\epsilon(\Delta$ temp+ Δ precip+land use)	0.04	0.30	0.34	0.32	+	+	+
Killdeer	0.06	60	$\epsilon(\Delta$ temp+ Δ precip+land use)	0.10	0.26	0.37	0.27	+	+	+
N. Rough-winged Swallow	-0.02	19	$\epsilon(\Delta$ temp+ Δ precip+land use)	0.01	0.41	0.33	0.25	+	+	-
Mourning Dove	-0.04	20	unassigned	0.36	0.38	0.05	0.20	-	-	-
Yellow Warbler	-0.12	158	unassigned	0.35	0.16	0.29	0.21	+	+	+
Purple Finch	-0.15	44	unassigned	0.35	0.27	0.21	0.17	-	-	-
Swainson's Thrush	-0.11	5	unassigned	0.35	0.04	0.28	0.33	+	-	-
Spotted Towhee	0.22	66	unassigned	0.34	0.18	0.25	0.22	-	-	-
American Robin	0.04	36	unassigned	0.33	0.29	0.18	0.21	-	+	-
White-crowned Sparrow	-0.06	15	unassigned	0.31	0.22	0.18	0.28	+	+	-
Yellow-breasted Chat	-0.09	89	unassigned	0.30	0.24	0.21	0.24	+	-	-
Spotted Sandpiper	-0.02	55	unassigned	0.28	0.23	0.23	0.26	+	+	+
American Crow	-0.19	32	unassigned	0.28	0.13	0.24	0.35	-	-	-
Cooper's Hawk	-0.04	95	unassigned	0.22	0.23	0.29	0.25	+	-	-

Table 12. Factors Affecting Colonization and Extinction Dynamics Were Not Significantly Associated With Species' Taxonomy, Foraging Guild, or Life History Traits, as illustrated by the χ^2 Test Results.

Species Groupings	γ		ϵ	
	χ^2	p-value	χ^2	p-value
Taxonomy (passerine, woodpecker, raptor, other)	25.72	0.11	18.75	0.41
Foraging guild (granivore, insectivore, generalist, other)	13.92	0.73	16.95	0.53
Passerine (resident, nonresident)	10.13	0.12	8.30	0.22
Nest type (cup, cavity, other)	13.17	0.36	10.97	0.53
Clutch size	6.25	0.40	10.85	0.09
Body mass	6.48	0.37	8.80	0.19

Figure 1. Map of the 70 Avian Resurvey Sites That Comprised the Grinnell Resurvey Project in the California Coast Range, California, USA.

See Table 1 for site information.



Figure 2. Mapped Values of the Three Predictor Variables Used to Test Colonization and Extinction Dynamics. Plotted at each of the 70 resurvey sites are: A. change in mean annual temperature, B. change in annual precipitation, and C. land use intensity.

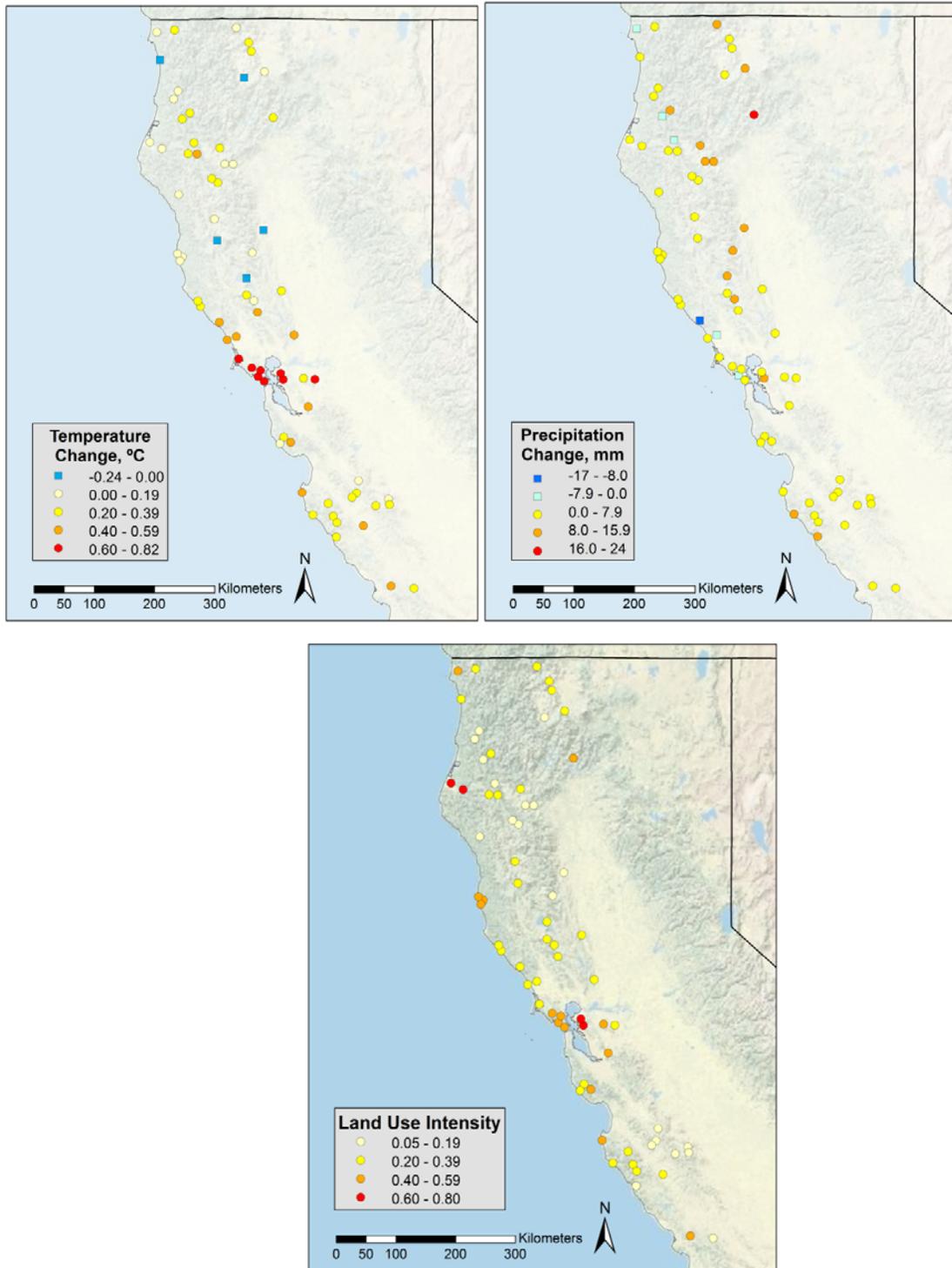


Figure 3. Change in the Proportion of Sites Occupied by a Species Between the Modern and Historic Eras for Each of the 100 Modeled Bird Species. Occupancy declined on average by -0.03, but ranged from -0.41 to 0.63.

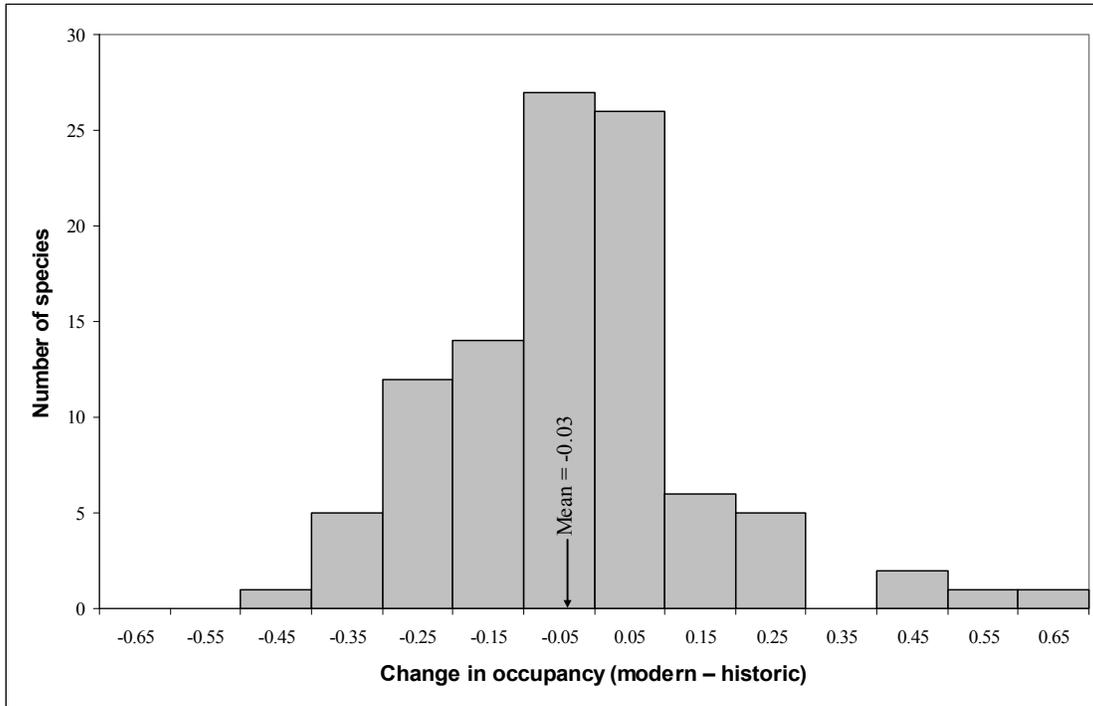
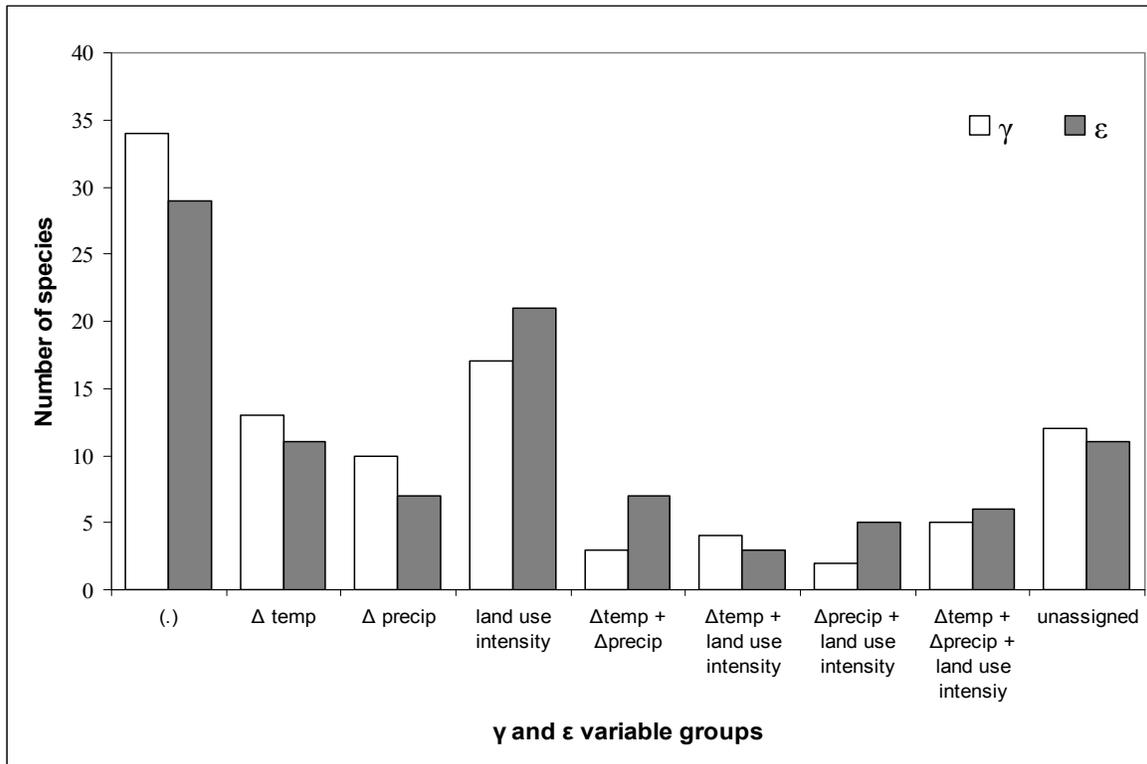


Figure 4. The Number of Species Whose Local Colonization and Extinction Dynamics Were Best Explained by Climate and Land Use Covariates Using Cumulative AICc Weights. To be assigned as an explanatory covariate, the best ranked model must exceed other covariates by 0.1 (see Methods).



APPENDIX A

Appendix 1: The 220 Bird Species Detected in Historic or Modern Surveys

Appendix 2: The 95 Percent Confidence Model Set (summed weights) of the 324 Models: Colonization (γ) was either parameterized with covariates or with a constant probability, and extinction (ϵ) was always parameterized as a constant probability

Appendix 3: The 95 Percent Confidence Model set (summed weights) of the 324 Models: Colonization (γ) was always parameterized as a constant probability, and extinction (ϵ) was either parameterized with covariates or with a constant probability

Appendix 4: Maps of Each Species' Turnover Dynamics

Appendix 5: The Probability of Occupancy for Historic (ψ_1) and Modern (ψ_2) Surveys at 70 Sites for the 100 Species Whose Site Occupancy Dynamics Modeled.